BULLETIN

OF CARNEGIE MUSEUM OF NATURAL HISTORY

DAWN OF THE AGE OF MAMMALS IN ASIA

Edited by

K. CHRISTOPHER BEARD *and* MARY R. DAWSON

Section of Vertebrate Paleontology

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Jay Apt, *Director*

Cover illustration: A fossiliferous outcrop of the middle Eocene Heti Formation in southern Shanxi Province, People's Republic of China. The Yellow River drainage and mountains in northern Henan Province are visible in the distance. Paleontologists from the Carnegie Museum of Natural History and the Institute of Vertebrate Paleontology and Paleoanthropology (Chinese Academy of Sciences) have undertaken rescue field operations in this area from 1994–1997, in anticipation of a new hydroelectric dam on the Yellow River downstream (see papers by Beard and Dawson and Tong in this volume).

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PREFACE

The immense area of Eurasia today encompasses over one-third of the Earth's land surface (roughly 54,430,000 km²). The diversity of habitats available to the more than 700 species of land mammals endemic to this area (Ellerman and Morrison-Scott, 1966) covers the full range of terrestrial ecosystems from tundra through tropical rainforest. Deserts cover wide areas of Eurasia, which contains not only the lowest elevations exposed on dry land but also its highest mountain range, the Himalayas.

At the beginning of the interval addressed by papers in this symposium, about 80 million years ago, Eurasia was not one continuous land mass. Rather, the area that is now roughly Asia was separated from the region that today comprises Europe by a wide epicontinental seaway, the Turgai Straits, that linked the Arctic and Tethys seas. The great Tethys Sea formed a vast embayment in the south of the present land area (Smith et al., 1994). Tectonic forces had raised the southern part of the Tibetan Plateau to an elevation of 3 to 4 km, leading to development of marked topography in that region (Murphy et al., 1997). The following 50 million years witnessed massive changes in the areas both west and east of the Turgai region. In its drive northward, the Indian plate continued its subduction under Asia, leading to further changes in the Asian land mass. Eurasian mountains tend to be east–west oriented, in relation to the dominant physical forces creating the Alpine–Himalayan chain. The European region remained an area of shifting coastlines through the Paleogene. Changes in the climatic regime for the area accompanied alterations in the distribution of Tethys and elevation of the mountains. Increasing desertification characterized central Asia.

As these changes occurred, Asia served as a vast laboratory for mammalian evolution. Some results of this evolution are the object of this volume. Part of this occurred while dinosaurs were still the dominant land vertebrates; latter parts occurred after the dinosaurs were gone, and the challenge of filling vacated niches was open to the survivors. At various times being considered here, Asia served as a centrally located biogeographic link with Europe, the south Asia–Australian region, Africa, and North America.

EARLIER INVESTIGATIONS OF FOSSIL MAMMALS IN ASIA

The concept of fossils as remains of previous life is certainly not a new one in Asia. The first recognition of their organic nature occurred in China as early as the Tang dynasty in the eighth century (Needham, 1956), but as with most scientific studies of fossils, the development of mammalian paleontology in Asia has been essentially a 19th- and 20th-century phenomenon. During this time studies of fossil mammals in Asia have had a relatively adventurous record. Perhaps the real pioneer field paleontologists were the Chinese drug merchants who collected vertebrate fossils, mostly of Quaternary age, calling them dragon bones and dragon teeth. Physicians prescribed these in powdered form (sometimes soaked in alcohol) for a variety of complaints. The less-applied study of fossil vertebrates can be ascribed to early Western travelers and missionaries. A British scholar, Hugh Falconer, reported in 1846 on Quaternary mammals from Tibet (Zhou, 1981). Owen (1870) described Chinese fossil mammals, mostly Quaternary forms from drugstores. Gaudry (1872) reported on Quaternary mammals collected by the French Abbé David from north of Beijing. Schlosser (1903) produced the first relatively comprehensive treatment of Chinese fossil mammals, based on a large collection purchased by a German Dr. Harberer in Chinese drug stores (Granger, 1932:510). Another early report was that of V. A. Obruchev (1893), who discovered a "rhinoceros" tooth in Mongolia in 1892.

So far as the Cretaceous and Paleogene are concerned, the early 20th century was a time of contributions by both non-Asian specialists who were working in Asia for a variety of reasons and by Asian paleontologists. One of the earliest important contributors was the remarkable J. G. Andersson of Sweden, who, after a productive geological career in his homeland, became mining advisor to the Chinese government in 1914. He also was Curator of the Museum of the Geological Survey of China and worked closely with its Director, V. K. Ting, and Vice-Director, W. H. Wong. In 1916 Andersson discovered the first Eocene mammals to be found in China, along the north bank of the Huang He (Yellow River) in southern Shanxi Province. The first locality found, the famous "River Section" or "Lo-

cality 1," was investigated by Andersson and later Zdansky (Andersson, 1923). Eocene fossil-bearing strata on the south side of the river, near the village of Rencun, were also studied by Zdansky. During the course of his work in China, which also focused on Neogene localities, Andersson formed a network of Swedish and other missionaries and other foreign residents to keep him informed of new fossil sites. In addition, he developed a campaign of learning of significant localities for vertebrates from Chinese druggists. Swedish involvement in studies of Chinese fossil mammals continued when Sven Hedin, the great Swedish explorer and geographer, organized an expedition to Inner Mongolia and Xinjiang in 1927. Birger Bohlin of Uppsala was hired as the paleontologist for the expedition. Bohlin's work in Nei Mongol, Gansu, and Tsaidam between 1929 and 1933 yielded outstanding results (Mateer and Lucas, 1985). An important series of studies on Paleogene fossil mammals discovered during the course of this expedition were produced as reports of the Sino–Swedish Expedition, and published in *Palaeontologia Sinica* of the Geological Survey of China.

French missionaries continued in the 20th century the earlier work of Abbé David. In 1923 Pierre Teilhard de Chardin went to China to work with Père Licent. Oligocene faunas from Saint-Jacques in Ordos (Ningxia) as well as Neogene mammals formed the core of his investigations (Teilhard de Chardin, 1926; Teilhard de Chardin and Leroy, 1942). Teilhard became scientific advisor to the Geological Survey of China and stayed in China until 1946. Most of his later work concerned Neogene hominids.

The entry of American paleontologists into the fossil fields of Asia resulted from both scientific and exploratory enthusiasms. Two eminent paleontologists at the American Museum of Natural History, H. F. Osborn and W. D. Matthew, were especially impressed with the Holarctic as, in Osborn's term, "the Grand Center of Evolution" for mammals (Osborn, 1910; Matthew, 1915). It was natural that their interests should turn to the relatively little-explored fossil deposits of Asia. Their cause was joined enthusiastically by Roy Chapman Andrews, explorer and adventurer. The planned expeditions had an ambitious focus: "The main problem was to be a study of the geologic history of central Asia; to find whether it had been the nursery of many of the dominant groups of animals, including the human race; and to reconstruct its past climate, vegetation and general physical conditions, particularly in re-

lation to the evolution of man" (Andrews, 1932:5). Field seasons of the Central Asiatic Expeditions to Mongolia in 1922, 1923, 1925, 1928, and 1930 were extraordinarily successful. Cretaceous and Tertiary vertebrates were found that opened new vistas for studies of mammalian phylogeny and paleobiogeography.

An important landmark for investigations of fossil mammals in China was the publication in 1927 by Chungchien (C. C.) Young (Yang Zhongjian) on fossil rodents of North China, written while he was a student in Munich. This was the first paper published by a Chinese vertebrate paleontologist. Young's career continued in China, where in 1929 he was one of the founders of the Palaeontological Society of China and of the Laboratory of Cenozoic Studies. In 1953 the Laboratory became the Institute of Vertebrate Paleontology and Paleoanthropolgy (IVPP) under the direction of Young and Pei Wenchung (Zhou, 1981). These scholars led the IVPP through both difficult and productive times. "Scientific work all over China had been severely disrupted from 1966 to 1976, in the period of the 'Cultural Revolution,' when most research work ceased, publication of scientific results was reduced to a trickle, and communications of Chinese scientists with their colleagues abroad were severely restricted. The removal of these repressive measures in 1976 triggered a tremendous surge of scientific activities, resulting in a veritable deluge of high quality publications in all branches of paleontology in an ever increasing number of publication outlets" (Teichert and Yin, 1981:vii). Following Young's death in 1979, Zhou Minzhen became director of the increasingly productive IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, 1994).

The Academy of Sciences of the USSR sent three paleontological expeditions under the direction of J. A. Efremov (1946, 1948, 1949) to Mongolia, and in 1959 and 1960 the Academy of Sciences of the USSR and that of the People's Republic of China joined together in paleontological expeditions to Inner Mongolia, under the leadership of Rozhdestvensky and Zhou. In another cooperative venture, the Polish Academy of Sciences and the Academy of Sciences of the Mongolian People's Republic collected important Cretaceous and early Tertiary mammals in the course of expeditions between 1963 and 1965 in the southern Gobi and western Mongolia (Kielan-Jaworowska and Dovchin, 1968).

Farther south in Asia, the Paleogene of Burma

has long been known for important faunas. The Pondaung fauna of Burma was studied first by the English paleontologist G. E. Pilgrim and later by American paleontologists (Colbert, 1938). Pilgrim also described the first Eocene mammals of the Indian subcontinent. Since the late 1950s further work by international teams of paleontologists have developed important faunas, including marine mammals, from both Pakistan and India.

During this long interval of paleontological investigations in Asia, in spite of changing political pressures, shifting national boundaries, and fluctuating economic conditions, paleontologists have not wavered in their goal of searching out the history of life.

THE SYMPOSIUM: DAWN OF THE AGE OF MAMMALS IN ASIA

A long history of paleontological investigations in Asia plus the increased pace of paleontological discoveries in the past 15 to 20 years suggested that a review of recent ideas on early mammals of Asia was due. Accordingly, this theme became the subject of a symposium that took place on November 1, 1995, during the 55th annual meeting of the Society of Vertebrate Paleontology in Pittsburgh, Pennsylvania. Brought together here are results of some current phylogenetic, stratigraphic, and paleobiogeographic investigations. One major review paper (Beard) echos the overall theme of the symposium and strongly emphasizes the importance of Asia in the overall development of mammals. Phylogenetic results include discussions of a variety of Asian mammals (Dashzeveg et al., an endemic Glires; Gingerich et al., and Thewissen and Hussain, marine mammals; Dawson and Tong, an early cricetid rodent). Many of the localities discussed are relatively new to paleontological research (e.g.,

Nessov et al., Cretaceous of Uzbekistan; Maas et al., the Eocene Kartal Formation of Turkey), while others are refined investigations on previously known faunas (e.g., Meng et al., the Bayan Ulan fauna; Beard, the River Section of Shanxi). A major theme is correlation of the Asian faunas, a field fraught with difficulties in a region with few intercalations of marine deposits and few radiometric dates. A comparison of the opinions of Wang et al., Ting, Tong and Wang, and Averianov and Godinot on Paleocene and Eocene biostratigraphy shows that much remains to be done before confidence can be placed in these shifting sands. Perhaps more convincing results, although less far reaching, can be found in the relatively local stratigraphic sections reported by Lucas et al. and Emry et al.

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Mary R. Dawson
September 23, 1997
Pittsburgh, Pennsylvania, USA

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EAST OF EDEN: ASIA AS AN IMPORTANT CENTER OF TAXONOMIC ORIGINATION IN MAMMALIAN EVOLUTION

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ABSTRACT

The continuity of phylogenetic descent requires that sister taxa originate at the same time and in the same place. Phylogenetic constraints on biostratigraphy and paleobiogeography are imposed by this simple rule, but these relationships have frequently been overlooked or underappreciated. Highly corroborated paleobiogeographic hypotheses are supported by both phylogenetic and biostratigraphic datasets. Based on this approach to paleobiogeographic reconstruction, Asia is identified as the most likely ancestral area for a large number of placental mammal clades, including Perissodactyla, Artiodactyla, Cetacea, Dinocerata, Tillodontia, Arctostylopidae, Pantodonta, Coryphodontidae, Rodentia, Alagomyidae, Lagomorpha, Primates, and Hyaenodontidae.

Contrary to many traditional notions regarding North American mammalian evolution, few higher-level mammal taxa seem to have originated in North America. Rather, North America has functioned primarily as a biogeographical cul-de-sac of Asia since at least late Cretaceous time. Iterative dispersal of higher-level mammal clades into North America from Asia has been the dominant mode of modernization of the North American mammalian biota throughout the Cenozoic Era. This "East of Eden" model agrees with paleogeographic reconstructions, which severely constrain potential source areas for mammalian immigrants to North America subsequent to early Eocene rifting in the North Atlantic. As in the case of the Grand Coupure and the Great American Interchange, East of Eden dispersal is characterized by immigrant taxa hailing from the larger landmass (in this case, Asia) being far more likely to colonize the smaller landmass (in this case, North America) than vice versa.

Three closely staggered East of Eden dispersal events during the interval spanning late Tiffanian (Ti5) through basal Wasatchian (Wa0) are interpreted as the result of a single sustained climatic warming trend. Progressive reduction of latitudinal temperature gradients over the course of this late Paleocene–early Eocene interval allowed three consecutive waves of Asian endemic mammals to disperse across Beringia and successfully colonize North America: Dinocerata and Arctostylopidae (Ti5); Rodentia, Tillodontia, and Coryphodontidae (Clarkforkian; Cf1); and Perissodactyla, Artiodactyla, Primates, and Hyaenodontidae (Wa0).

In light of the East of Eden paleobiogeographic model, previous attempts to correlate early Paleogene Asian Land Mammal Ages (ALMAs) have probably underestimated their antiquity. The Gashatan ALMA probably correlates with the latter half of the Tiffanian and possibly the earliest part of the Clarkforkian. The Bumbanian ALMA may correlate with the remainder of the Clarkforkian and the early part of the Wasatchian.

INTRODUCTION

"We are thus brought to the question which has been largely discussed by naturalists, namely, whether species have been created at one or more points of the earth's surface. Undoubtedly there are many cases of extreme difficulty in understanding how the same species could possibly have migrated from some one point to the several distant and isolated points, where now found. Nevertheless the simplicity of the view that each species was first produced within a single region captivates the mind. He who rejects it, rejects the *vera causa* of ordinary generation with subsequent migration, and calls in the agency of a miracle." (Charles Darwin, *The Origin of Species*, Sixth Edition, p. 418)

The phylogeny and adaptive radiation of late Cretaceous and early Cenozoic mammals took place on a dynamic geographical backdrop that was unlike that familiar to us today, but one that also differed from the monotonous conditions afforded by the supercontinent of Pangaea (and subsequently, Laurasia and Gondwanaland) earlier in the Mesozoic.

This constantly changing geographical setting undoubtedly influenced the course of mammal phylogeny, perhaps in ways more numerous than one can easily imagine (cf. McKenna, 1983*a*). Indeed, the breakup of large Mesozoic landmasses into smaller continental plates has itself been cited as a factor underlying the radiation of early mammals and birds (Hedges et al., 1996). Regardless of whether or not the model of Hedges et al. (1996) proves to be accurate, it is clear that geographic segregation of certain landmasses resulted in marked endemism in their native mammal faunas. A prime example is the celebrated "splendid isolation" of South America, which supported an adaptive radiation of mammals remarkable both for its endemism and its evolution of basic bauplans strikingly convergent on those found elsewhere in Mammalia (e.g., Simpson, 1980; Cifelli, 1993).

However, even in the case of island continents like South America, new paleontological discoveries are demonstrating that faunal and geographic links to other continents were at times both striking and pronounced (de Muizon and Marshall, 1991, 1992; Pascual et al., 1992; Woodburne and Case, 1996).

Scientific attempts to reconstruct the biogeographical history of mammals, particularly over the critical late Cretaceous–early Cenozoic interval during which much of mammalian higher-level taxonomic diversity was generated, have lagged far behind attempts to reconstruct their phylogeny. This delay is natural inasmuch as knowledge of phylogeny is a prerequisite for assessing such second-order phenomena as the historical biogeography of a clade. Yet I will argue below that the reciprocal illumination between phylogeny and biogeography has been significantly underexploited by paleomammalogists in recent years. My goal here is to explore some of the logical interrelationships among phylogeny, biogeography, and biostratigraphy as they relate to the early evolution of mammals in Asia.

PHYLOGENY AND PALEOBIOGEOGRAPHY

Biogeographic hypotheses are implicit within all phylogenetic hypotheses. That is, by positing that two clades are sister taxa, one also postulates that these clades originated in the same geographic region. Furthermore, because speciation is a local (rather than global) phenomenon, it is theoretically possible to reconstruct the region of origin of any particular clade at some level of geographic precision below that of the Earth as a whole. The level of geographic precision that may be desired in reconstructing the region of origin of a given clade varies from taxon to taxon. For example, reconstructing the continent on which the living marsupial genus *Macropus* originated is biogeographically uninteresting because it and its immediate relatives are, and apparently always have been, confined to Australia and nearby islands. On the contrary, identification of the continental landmass that originally spawned all Metatheria is hotly debated, and resolution of this issue would represent a real advance in our knowledge of mammalian historical biogeography (cf. Szalay and Trofimov, 1996). As in the latter case, it is currently unrealistic to attempt to specify the region of origin of such higher-level taxa as living and extinct orders of placental mammals at geographic scales below that of the continent.

Operationally, paleobiogeographic hypotheses regarding the region of origin of a clade are contingent on phylogenetic reconstructions of that clade and closely related outgroups. In terms of parsimony alone, it is possible to treat the known geographic ranges of living and fossil taxa as "characters" to be optimized at interior nodes on a cladogram (Fig. 1). Use of such biogeographic "characters" in phylogeny reconstruction is emphatically not advocated here, if for no other reason than to maintain the independence of phylogenetic and biogeographic datasets. Rather, a posteriori optimizations of these biogeographic "characters" at interior nodes on a cladogram can serve as working hypotheses regarding the area of origin of a clade. Such phylogenetically derived hypotheses regarding the region of origin of a clade are then available for further evaluation in the light of other relevant datasets. Examples of datasets that are useful for comparison with these phylogenetically derived biogeographic reconstructions include the fossil record of the clade and geophysical data pertaining to the likelihood of the clade's dispersal and/or vicariance. Ronquist (1997) has recently outlined a parsimony-based method for reconstructing geographic distributions at interior nodes of a cladogram that is similar in many ways to that employed here.

Highly corroborated hypotheses regarding the region of origin of a clade are those in which phylogenetically derived biogeographic reconstructions are unambiguous and are congruent with other datasets, particularly a dense fossil record for the clade. In cases in which there is strong congruence between phylogenetically derived biogeographic reconstructions and the fossil record, consensus regarding the region of origin of a clade can actually be far stronger than that regarding the phylogeny of a clade. For example, it is virtually universally accepted that the human clade (that is, living humans + all fossil species that are more closely related to humans than to our nearest living outgroups, *Pan* and *Gorilla*) originated in Africa (e.g., Wood, 1992; Strait et al., 1997). This consensus is based on 1) unambiguous optimizations that reconstruct Africa as the ancestral geographic range at the interior node defining the human clade (i.e., all basal species within the human clade, as well as successive outgroups, are restricted to Africa); and 2) congruence between this phylogenetically derived biogeograph-
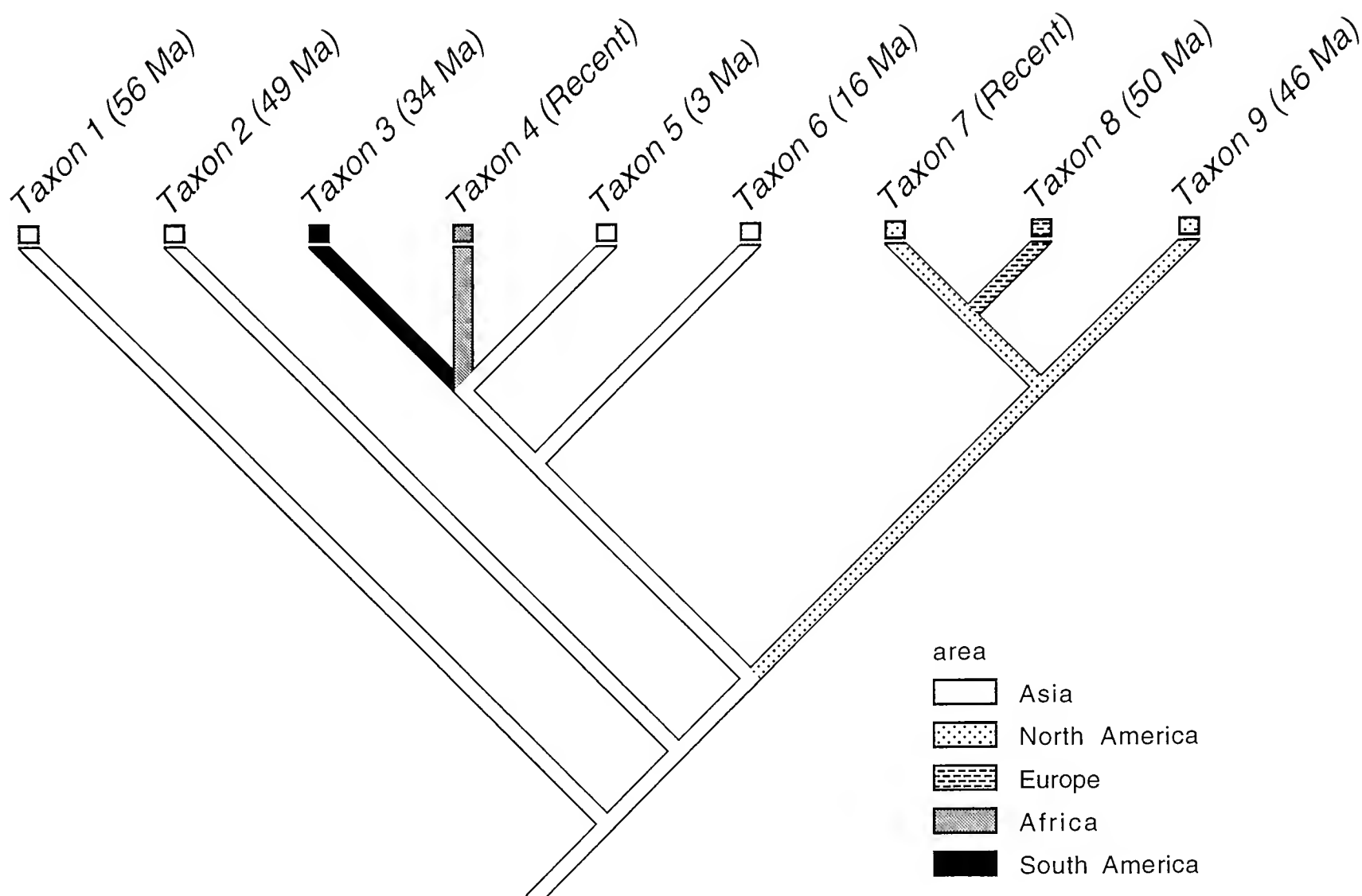
Fig. 1.—A phylogenetically derived biogeographic reconstruction for a hypothetical clade consisting of nine living and fossil taxa. Age of terminal taxa is shown in parentheses. Each terminal taxon is restricted to one of the five geographic areas (continents) shown at the lower right, as follows: taxa 1, 2, 5, and 6 are endemic to Asia; taxon 3 occurs in South America; taxon 4 occurs in Africa; taxa 7 and 9 are endemic to North America; taxon 8 occurs in Europe. A posteriori optimization of the geographic distributions of terminal taxa on this tree topology unambiguously reconstructs Asia as the continent on which the entire clade originated, with subsequent dispersal to South America (taxon 3), Africa (taxon 4), North America (ancestor of taxa 7, 8, and 9), and Europe (taxon 8). In this example, the phylogenetically derived biogeographic reconstruction is congruent with the fossil record because taxon 1 is both the oldest and most basal member of the clade.

ic reconstruction and the fossil record of the human clade, which is far older in Africa than elsewhere (cf. White et al., 1994). Importantly, the broad consensus regarding an African origin for the human clade is likely to withstand ongoing debate over details of this clade's phylogeny.

Although biogeographic reconstructions of the area of origin of a clade are operationally contingent on phylogenetic reconstructions of that clade, the possibility of reciprocal illumination between paleobiogeography and phylogeny remains. That is, biogeographic evidence that two clades that are thought to be sister taxa actually did originate in the same region can be viewed as corroborating the original phylogenetic hypothesis. For example, several anatomical lines of evidence support the monophyly of the supraordinal taxon Glires, which encompasses the orders Rodentia and Lagomorpha (e.g., No-

vacek et al., 1988; Novacek, 1990). Felicitously, the fossil record suggests that both Rodentia and Lagomorpha originated in Asia (e.g., Li and Ting, 1993; Meng et al., 1994). In this case paleobiogeographical data that are independent of the anatomical data on which Glires rests are consistent with a major prediction of Glires monophyly—that rodents and lagomorphs shared a common area of origin.

Alternatively, in cases in which taxa believed to be sister groups show discordant biogeographical patterns, the disjunct areas of origin inferred for the sister taxa require explanation. Frequently, apparent conflicts such as these can be attributed to the incompleteness of the fossil record (i.e., the sister taxa actually did share a common region of origin, but this is obscured by the vagaries of fossil preservation). This interplay between phylogeny and bio-

geography is analogous to that between phylogeny and the stratigraphic ranges of sister taxa (the "ghost lineage" concept of Norell [1992, 1993]; also see Weishampel [1996]). Less frequently among mammals, disjunct distributions may have resulted from large-scale geophysical processes causing vicariance. Of course, when evidence for the disjunct origination of taxa reputed to be sister groups is strong and seemingly inexplicable by the preceding criteria, it is always prudent to reassess the level of support for the phylogenetic reconstruction underlying the conflict.

WHY FOCUS ON ASIA?

Several paleogeographic and paleobiogeographic factors peculiar to Asia conspire to make it an ideal candidate to have served as an important theater of mammalian diversification during the late Cretaceous and early Cenozoic. These include the large area of contiguous terrestrial habitats subsumed within the Asian continent, the precocious development of varied environmental conditions there, and the central position occupied by Asia with respect to other continental landmasses during this interval of time.

GEOGRAPHIC AREA AND TAXONOMIC DIVERSITY

As recently reviewed by Rosenzweig (1995), larger areas support greater biotic diversity than do smaller areas. This ubiquitous ecological pattern holds over geographic scales ranging from islands within an archipelago to continents. Today, the vast Eurasian continent is the world's largest continuous region of dry land. Despite the ebb and flow of epicontinental seas, Asia probably maintained this status throughout much, if not all, of the Cenozoic (e.g., Smith et al., 1994). Hence, one can reasonably infer that the diversity of mammals inhabiting Asia during the late Cretaceous and early Cenozoic exceeded that on other continents at this time. Indeed, considerations of area alone may underestimate mammalian diversity on Asia because of the precocious development of faunal provincialism there.

As will become evident below, the vast area encompassed by the Asian landmass and the high taxonomic diversity of Cenozoic mammals inferred to have lived there resulted in numerous instances in which Asian endemic mammal taxa successfully colonized other landmasses. In agreement with MacArthur and Wilson's (1967) equilibrium theory, only rarely did exotic mammals from other landmasses successfully invade Asia.

PALEOENVIRONMENTAL HETEROGENEITY AND FAUNAL PROVINCIALISM

Evidence for faunal provincialism within Asia during the late Cretaceous and early Cenozoic is abundant, almost certainly reflecting the formation of highly divergent habitats there at this time. In particular, the semiarid to arid conditions that so typify central Asia today can be traced back to the Campanian, when extensive eolian dune fields developed in the Gobi Basin along the Chinese–Mongolian frontier (Eberth, 1993; Jerzykiewicz et al., 1993). This precocious development of relatively arid conditions in central Asia may have been tied to rejuvenation of the Tian Shan range, uplift of which began to cast a rain shadow over the Tarim and Turpan basins in Xinjiang as early as the early Cretaceous (Hendrix et al., 1992). In contrast to the persistently more xeric conditions in central Asia, more mesic habitats undoubtedly prevailed in lower-latitude parts of Asia and in areas nearer to the ancient coastlines of Tethys and the Pacific Ocean during much of the late Cretaceous and early Cenozoic (e.g., Tong, 1994).

Unsurprisingly, fossil mammal faunas from these latter areas can differ markedly from those derived from the more "classic" localities known from Mongolia and northern China. Examples of this phenomenon include: 1) the diversity of late Cretaceous "zhelestid" ungulatomorphs now known from coastal plain depositional settings in Uzbekistan, but which remain unknown from drier habitats in central Asia (Archibald, 1996; Nessov et al., 1998); 2) the apparent absence of multituberculates in numerous Paleocene basins of central and southern China, which contrasts with their relative abundance and diversity in Gashatan faunas of northern China and Mongolia (Sloan, 1987; Meng et al., 1998; Wang et al., 1998); 3) the presence of numerous taxa showing North American affinities (including Epoicotheriidae, Carpolestidae, Paromomyidae, Paramyidae, and others) in the Bumbanian Wutu fauna of Shandong Province, China (Tong and Wang, 1998), none of which are recorded in the similar-aged mammal fauna known from the Bumban Member of the Naran Bulak Formation in southern Mongolia; and 4) the presence of such unusual and distinctive taxa as the primates *Tarsius*

eocaenus, *Macrotarsius*, and *Adapoides*, didelphid marsupials, and palaeotheriid perissodactyls in the middle Eocene Shanghuang fissure fillings of southern Jiangsu Province (Beard et al., 1994; Qi et al., 1996), which contrasts with their absence or extreme rarity in similar-aged faunas from the interior of the Asian continent.

Despite comparatively good geographic representation of early Cenozoic mammal-bearing sites within China, a potentially critical part of the early Cenozoic record of Asian mammal evolution continues to elude us. That is, aside from the late Eocene Pondaung fauna of Burma (e.g., Colbert, 1938; Holroyd and Ciochon, 1995) and the roughly coeval Krabi fauna of southern Thailand (e.g., Ducrocq et al., 1995, 1996; Chaimanee et al., 1997), we have no knowledge of the late Cretaceous and early Cenozoic mammals of southeastern Asia. Judging from its Recent biota, this area holds great promise as an important theater of mammalian phylogeny and diversification. At the very least, southeastern Asia has served as a Neogene refugium for such ancient mammalian clades as Tupaiidae, Galeopithecidae, and Tarsiidae (Ducrocq et al., 1992; Beard, 1998). Should significantly earlier mammalian faunas be recovered from this region, they too can be expected to differ from those known from more interior regions of Asia.

PALEOGEOGRAPHIC LINKS WITH OTHER CONTINENTS AND LANDMASSES

Among the three Laurasian continents of Europe, Asia, and North America, it is fair to characterize Asia as playing a central role in terms of paleogeography and paleobiogeography (Smith et al., 1994). That is, following the early Eocene rifting in the North Atlantic that ultimately separated northwestern Europe from Greenland (Ritchie and Hitchen, 1996), overland dispersal among Laurasian continents was (at least intermittently) possible between Asia and Europe and between Asia and North America, but not directly between North America and Europe. Cenozoic dispersal between Asia and the other two Laurasian continents must have been controlled largely by eustatic sea level and climate, as opposed to large-scale tectonics. The Obik Seaway east of the Ural Mountains formed a marine barrier between Asia and Europe during much of the early Paleogene (McKenna, 1983a; Smith et al., 1994), while the high northern latitude position of the Beringian region acted as a strong filter between Asia and North America that was especially dependent on climatic conditions (see below).

In contrast to the climatically and eustatically mediated relationships between Asia and other Laurasian landmasses, paleogeographic links between Asia and remnants of Gondwanaland were mainly dependent on large-scale tectonics. The most obvious of these resulted from the collision between the Indian subcontinent and the southern margin of Asia, which occurred during the early Paleogene (Beck et al., 1995). Krause and Maas (1990) view this collision as having highly significant biogeographic ramifications for the mammalian biota of Asia and other Laurasian landmasses, an opinion that is not endorsed here (see below).

Faunal data show unambiguously that paleobiogeographic links existed between Asia and the Afro–Arabian landmass during the Paleogene, but such critical factors as the mode of dispersal (at best via a strong filter, more likely via sweepstakes dispersal across the eastern Tethys), the timing of interchange, and the pathways by which dispersal occurred remain unknown (cf. Holroyd and Maas, 1994). Nevertheless, the distributions of certain mammal clades imply that these taxa were able to disperse between Asia and Afro–Arabia. In at least some cases dispersal between these landmasses may also have involved Europe as an intermediary. Taxa that are critical for demonstrating Paleogene dispersal between Asia and Africa include Primates (documented in Africa as early as late Paleocene; see Sigé et al., 1990), Proboscidea (documented in Africa as early as late Paleocene; see Gheerbrant et al., 1996), Rodentia (documented in Africa as early as middle Eocene; see Vianey-Liaud et al., 1994), Anthropoidea (documented in Africa as early as middle Eocene; see Godinot, 1994), Embrithopoda (documented in Africa as early as late Eocene; see Gagnon, 1997), and Anthracotheriidae (documented in Africa as early as late Eocene; see Ducrocq, 1995). Many, but not all, of these taxa are inferred to have originated in Asia (see next section). For early Asian records of Anthropoidea and Embrithopoda, see Beard et al. (1994, 1996) and Maas et al. (1998), respectively.

PHYLOGENETIC AND PALEONTOLOGICAL EVIDENCE FOR THE ORIGINATION OF MULTIPLE HIGHER-LEVEL MAMMAL CLADES IN ASIA

In light of the phylogenetic and paleontological criteria established earlier, hypotheses on the paleobiogeographic origins of selected higher-level clades of placental mammals are briefly evaluated here. Taxa that achieved widespread distributions and/or taxa that have proven to be biostratigraphically significant are emphasized, but this treatment is not meant to be exhaustive. Phylogenetically derived biogeographic reconstructions are obviously driven by the phylogenetic reconstructions upon which they are based. Because phylogenetic reconstructions for many of the taxa discussed below remain contentious, there are significant possibilities for refinement of these paleobiogeographic reconstructions in the future.

PROBOSCIDEA

Undoubted proboscideans are prominent members of early Tertiary mammal faunas in Africa (Mahboubi et al., 1984; Gheerbrant et al., 1996), and it seems highly probable that a major part of proboscidean evolution took place on that continent. However, anthracobunids, which are widely considered to be either basal proboscideans or proboscidean sister taxa, are restricted in their known distribution to the early Tertiary of Asia (Wells and Gingerich, 1983). Embrithopods, which are also frequently mentioned as basal members or sister taxa of Proboscidea (Court, 1992), are known from the early Tertiary of northern Africa and southwestern Asia (Maas et al., 1998). Because of these Asian records of basal proboscidean relatives, Fischer and Tassy (1993:232) concluded that, "The more evidence we gather, the less likely becomes the long-held assumption of an African endemic origin of hyracoids and proboscideans. Recent collections of stem tethytherians and stem proboscideans from Asia and China . . . now suggest an origin outside Africa and perhaps in Asia."

The phylogenetic reconstruction of Proboscidea and their fossil relatives published by Fischer and Tassy (1993), with emended relationships among advanced proboscideans as suggested by Court (1995) and Gheerbrant et al. (1996), implies unambiguously that the stem lineage for Proboscidea originated in Asia (Fig. 2). If so, early dispersal from Asia to Africa of the clade comprising advanced proboscideans is indicated by the late Paleocene age of *Phosphatherium escuilliei* (Gheerbrant et al., 1996). The fossil record of early proboscideans and their putative sister taxa does not contradict this phylogenetically derived biogeographic reconstruction, because such basal Asian taxa as the Nongshanian genus *Minchenella* are likely to be as old, if not older, than the earliest African proboscidean, *Phosphatherium*.

PERISSODACTYLA

Perissodactyls (excluding hyracoids, which are sometimes included in this order; cf. Prothero and Schoch, 1989) are common elements of most early Tertiary Holarctic faunas of basal Eocene or younger age. In contrast, FADs ("First Appearance Datums"; see Woodburne, 1996) for this order are much later in former Gondwanan landmasses. The FAD for perissodactyls in Africa is early Miocene, at which time both rhinocerotids and chalicotheriids are recorded (e.g., Coombs, 1989; Prothero et al., 1989). In South America the FAD for perissodactyls (in the form of Tapiridae and Equidae) is even younger, corresponding to the "Great American Biotic Interchange" about 2.5 million years ago (Webb, 1985).

Despite this evidence that perissodactyls inhabited the northern continents well before their first appearances in Gondwanan terrains, several workers have posited an origin for Perissodactyla in lower-latitude remnants of Gondwanaland. For example, Gingerich (1989:90) pointed to Africa as the likely ancestral homeland for Perissodactyla and other higher-level mammal taxa (including Artiodactyla, Primates, and Hyaenodontidae), citing resemblances between perissodactyls and African Eocene hyraxes as evidence in favor of this viewpoint. Biogeographically more complicated is the hypothesis advocated by Krause and Maas (1990:95–96), who suggested that perissodactyls and other higher-level mammal taxa (see above) may have originated on the Indian subcontinent prior to its collision with Asia. Under this hypothesis the Indian subcontinent functioned as a "Noah's Ark" (cf. McKenna, 1973, 1983a) during the late Cretaceous and Paleocene until it docked onto the southern margin of Asia sometime near the Paleocene–Eocene boundary. More traditional hypotheses regarding the landmass on which perissodactyls originated have cited all three Holarctic continents as prime suspects. However, earlier suggestions that perissodactyls may have originated in Central America or the southern part of North America (Morris, 1966; Sloan, 1969;
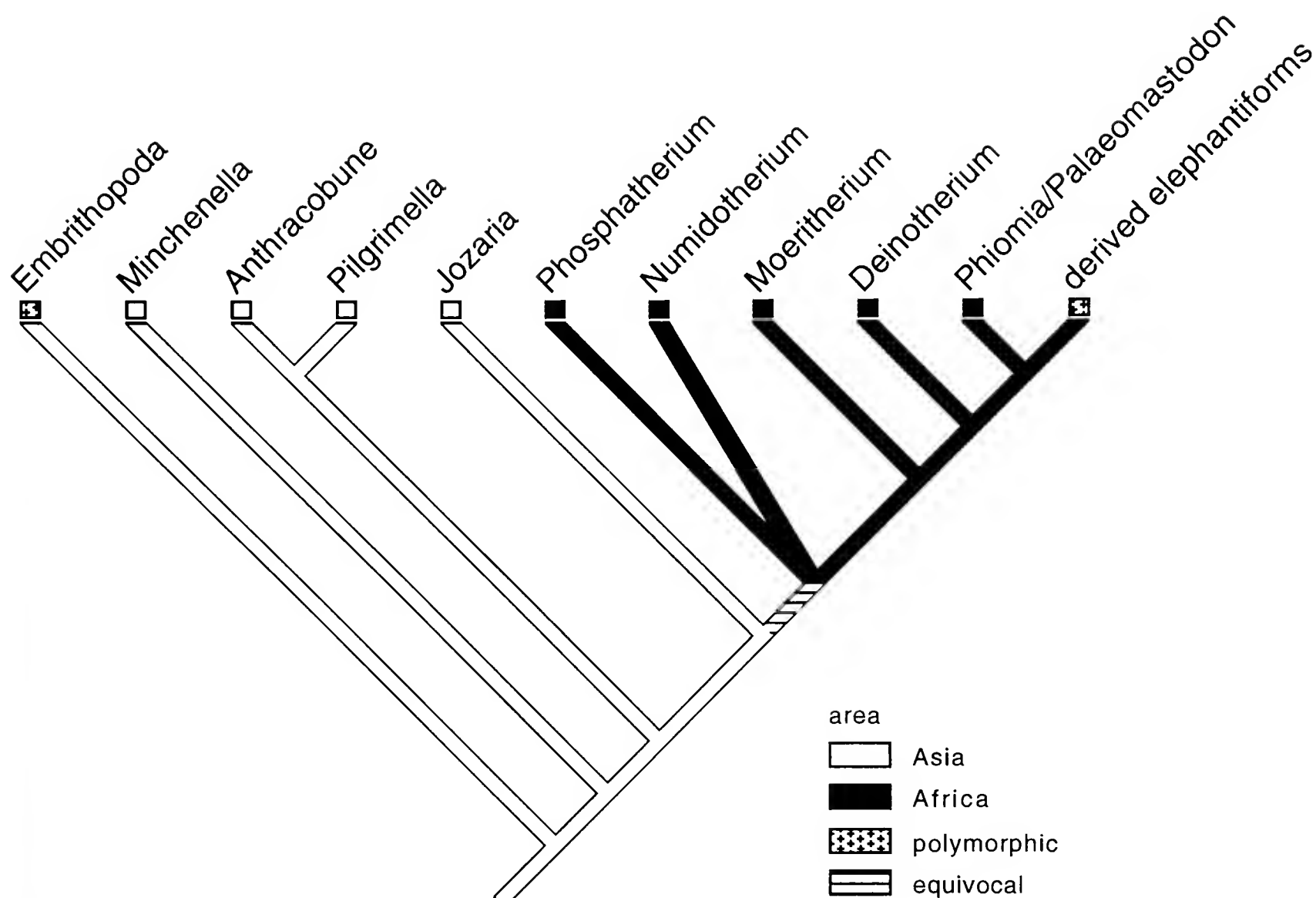
Fig. 2.—A phylogenetically derived biogeographic reconstruction for Proboscidea (sensu lato). The tree topology depicted here is based on Fischer and Tassy (1993), with emended relationships among advanced proboscideans as suggested by Court (1995) and Gheerbrant et al. (1996). Note that the stem lineage for Proboscidea is unambiguously reconstructed as endemic to Asia, followed by early dispersal of advanced proboscideans to Africa. In this and subsequent figures, terminal taxa occurring in more than one geographic region were coded as "polymorphic" for purposes of a posteriori optimization based on parsimony.

Gingerich, 1976; Schiebout, 1979) have now been largely abandoned (Gingerich, 1989; Krause and Maas, 1990). Similarly, although it has been suggested that the earliest North American perissodactyls dispersed to that continent from Europe (Hooker, 1980; Godinot, 1981, 1982), no recent worker has argued for a European origin for Perissodactyla (Krause and Maas, 1990). In contrast, the discovery of the Nongshanian perissodactyl-like mammal *Radinskya yupingae* in the Nanxiong Basin, Guangdong Province, China (McKenna et al., 1989), gives the hypothesis that perissodactyls originated in Asia renewed viability.

The past decade has witnessed a great resurgence in interest in reconstructing perissodactyl phylogeny, but no single phylogenetic reconstruction has achieved consensus. Furthermore, the possible sister-group relationship between Perissodactyla and Hyracoidea among living mammals continues to be debated (Fischer, 1989; de Jong et al., 1993; Fischer

and Tassy, 1993; Shoshani, 1993; Springer et al., 1997). Here, the Paleocene mammal *Radinskya yupingae* is accepted as the closest known sister group of Perissodactyla. Otherwise, the phylogeny for Perissodactyla published by Prothero and Schoch (1989:fig. 28.2), with emendations regarding equoid relationships as suggested by Hooker (1994), forms the basis for the phylogenetically derived biogeographic reconstruction undertaken here. Although frequent dispersal has greatly complicated the reconstruction of perissodactyl paleobiogeography, current knowledge of perissodactyl phylogeny indicates that Asia served as a persistent center of taxonomic origination throughout this clade's history (Fig. 3). In particular, the hypothesis that perissodactyls originated in Asia is unambiguously supported by the phylogenetic relationships depicted in Figure 3.

Three lines of evidence indicate that this phylogenetically derived biogeographic reconstruction is
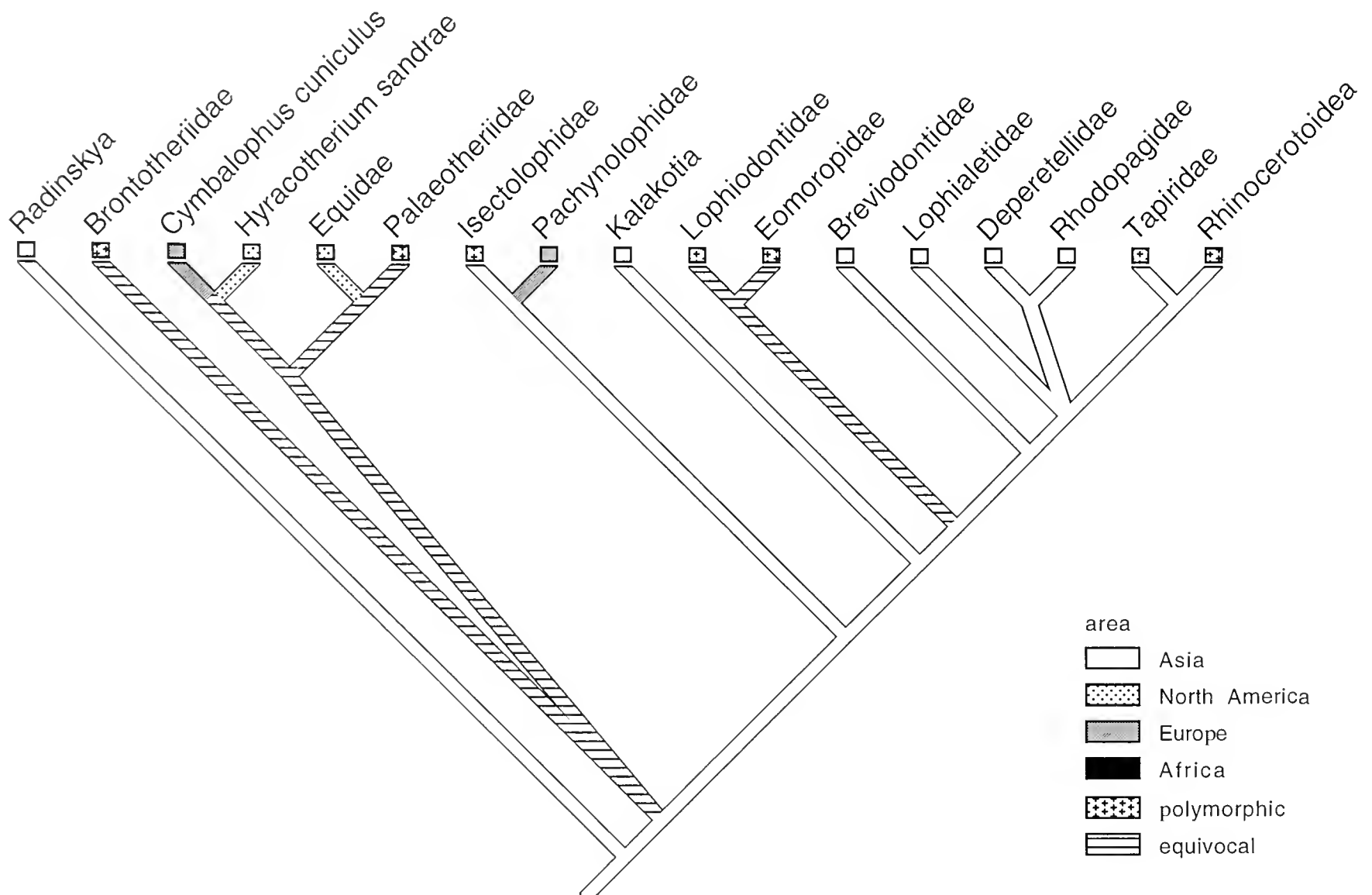
Fig. 3.—A phylogenetically derived biogeographic reconstruction for Perissodactyla. The tree topology depicted here is based on Prothero and Schoch (1989:fig. 28.2), with emendations regarding equoid relationships as suggested by Hooker (1994) and with *Radinskya yupingae* as the closest known sister group of Perissodactyla. Note that an Asian origin for Perissodactyla is unambiguously supported, and that Asia appears to function as a persistent center of origin for various perissodactyl clades throughout the history of the order.

concordant with the fossil record of perissodactyls. First, the Asian Nongshanian genus *Radinskya*, accepted here as the nearest sister group of perissodactyls, is undoubtedly older than perissodactyls from other continents (McKenna et al., 1989). Second, an indeterminate genus and species of perissodactyl showing morphological similarities to *Lambdotherium* occurs in the Bayan Ulan fauna, of Gashatan age, in Nei Mongol Autonomous Region, China (Meng et al., 1998). As is the case for *Radinskya*, the *Lambdotherium*-like perissodactyl from the Bayan Ulan fauna is clearly older than the earliest perissodactyls known from North America and Europe, which occur in basal Wasatchian and basal Sparnacian faunas, respectively (Meng et al., 1998; Wang et al., 1998; also see below). Finally, a growing diversity of Bumbanian perissodactyls in Asia (Chow and Li, 1965; Ting, 1993; Wang and Tong, 1996) may also be at least as old as the earliest perissodactyls known from North America and Europe (see below). Congruence between the phylo-

genetically derived biogeographic reconstruction depicted in Figure 3 and the fossil record of early perissodactyls underscores the strong support for the hypothesis that perissodactyls originated in Asia.

ARTIODACTYLA

As is the case for perissodactyls, artiodactyls are common elements of Holarctic mammalian faunas as early as the basal Eocene. The FAD for Artiodactyla in Africa is much later, consisting of anthracotheres from Nementcha, Algeria, and locality L-41, Fayum Depression, Egypt, that are thought to be late Eocene in age (Rasmussen et al., 1992; Ducrocq, 1995). The earliest South American artiodactyls date to roughly 2.5 million years ago (the "Great American Biotic Interchange"), when Camelidae, Cervidae, and Tayassuidae dispersed into South America from North America (Webb, 1985).

Previous hypotheses regarding the continent on which artiodactyls originated have varied largely

along the same lines as those regarding perissodactyl origins (see above). In particular, early suggestions (Sloan, 1969; Gingerich, 1976; Schiebout, 1979) that artiodactyls may have originated in either the southern part of North America or in Central America are no longer supported (Gingerich, 1989; Krause and Maas, 1990). Morphologically primitive European species of the early artiodactyl *Diacodexis* are known (Godinot, 1978, 1981; Estravis and Russell, 1989; Smith et al., 1996), suggesting to some authors that the earliest North American artiodactyls dispersed to that continent from Europe (Godinot, 1981, 1982; Estravis and Russell, 1989; Smith et al., 1996). However, because of the abrupt (and possibly synchronous) appearance of artiodactyls near the beginning of the Eocene in Europe and North America, most recent workers favor an origin for Artiodactyla outside both of these continents. As a result, an African origin for artiodactyls was proposed by Estravis and Russell (1989) and Gingerich (1989), despite the very late FAD for artiodactyls on that continent. Alternatively, Krause and Maas (1990) favored an artiodactyl birthplace on the late Cretaceous–early Tertiary Noah's Ark formed by the Indian subcontinent. Finally, study of the basal artiodactyl species *Diacodexis pakistanensis* led Thewissen et al. (1983) to propose an Asian origin for the order.

Assessing the early historical biogeography of artiodactyls on the basis of phylogenetic data is severely constrained by the absence of recognizable sister taxa for the order. Early suggestions that artiodactyls evolved from arctocyonid condylarths (Sloan, 1969; Van Valen, 1971) are now largely discounted (Rose, 1987). More recent studies cite Cetacea (+ Mesonychidae) as a potential sister group to Artiodactyla, or even as a nested clade within the suiform radiation (Irwin and Árnason, 1994; Philippe and Douzery, 1994; Randi et al., 1996). Until sister taxa of artiodactyls are more firmly established, phylogenetically derived biogeographic reconstructions for the order are best restricted to the analysis of ingroup relationships alone. Phylogenetic relationships among the diversity of living and fossil taxa of artiodactyls continue to be debated, but recent overviews agree that the fundamental dichotomy among Artiodactyla is that between Recent pigs, peccaries, hippopotamuses, and their fossil allies on the one hand, and all other artiodactyls on the other (Gentry and Hooker, 1988; Miyamoto et al., 1993). Allocation of the fossil taxa traditionally included in the basal, paraphyletic family Dichobunidae to the Selenodontia or Neoselenodontia has

been advocated by Gentry and Hooker (1988). This phylogenetic reconstruction is followed here, primarily because it is consistent with the advanced, neoselenodont-like postcranial anatomy known for *Diacodexis* (Rose, 1982, 1985). In order to simplify the analysis, only basal dichobunids are included to represent the diverse Neoselenodontia here.

Based on the phylogenetic reconstruction of basal neoselenodontians by Smith et al. (1996:fig. 1) and that for suiforms published by Gentry and Hooker (1988:fig. 9.8), biogeographic reconstruction of the continent on which artiodactyls originated is equivocal (Fig. 4A). Europe and Asia emerge as equally parsimonious optimizations for the basalmost node on the artiodactyl cladogram, as they do for the nodes at the base of the suiform and neoselenodontian radiations, respectively. Comparing the result from this phylogenetically derived biogeographic reconstruction with the fossil record of artiodactyls provides modest support for the view that Asia, rather than Europe, was the continent on which artiodactyls originated. Foremost among the fossil evidence supporting an Asian origin for artiodactyls is the unnamed taxon of basal suiform known from the Bumbanian Wutu fauna of Shandong Province, China (Tong and Wang, 1998). This critical taxon was not included in the phylogenetically derived biogeographic reconstruction undertaken here, because its phylogenetic position with respect to other suiforms has not yet been evaluated in detail. However, its great age and primitive anatomy open the possibility that the Wutu suiform comprises the sister group of all other suiforms. If so, addition of this taxon to the phylogenetically derived biogeographic analysis undertaken here would throw the weight of parsimony to the side of Asia as the unequivocal site of origin for both Suiformes and Artiodactyla (Fig. 4B). Indeed, an Asian origin for Suiformes is virtually inescapable in any case. Not only is the Bumbanian record from Wutu far older than any suiform known from other continents, but most family-level taxa of suiforms are widely acknowledged to have arisen in Asia. These include Anthracotheriidae (e.g., Suteethorn et al., 1988; Ducrocq, 1994a, 1995; Holroyd and Maas, 1994), Entelodontidae (e.g., Lucas and Emry, 1996), and Tayassuidae (e.g., Ducrocq, 1994b). Although supporting evidence remains weak, an Asian origin for Artiodactyla is the most likely hypothesis given current knowledge.

CETACEA

Following their acquisition of fully marine habits, cetaceans rapidly dispersed to achieve their current
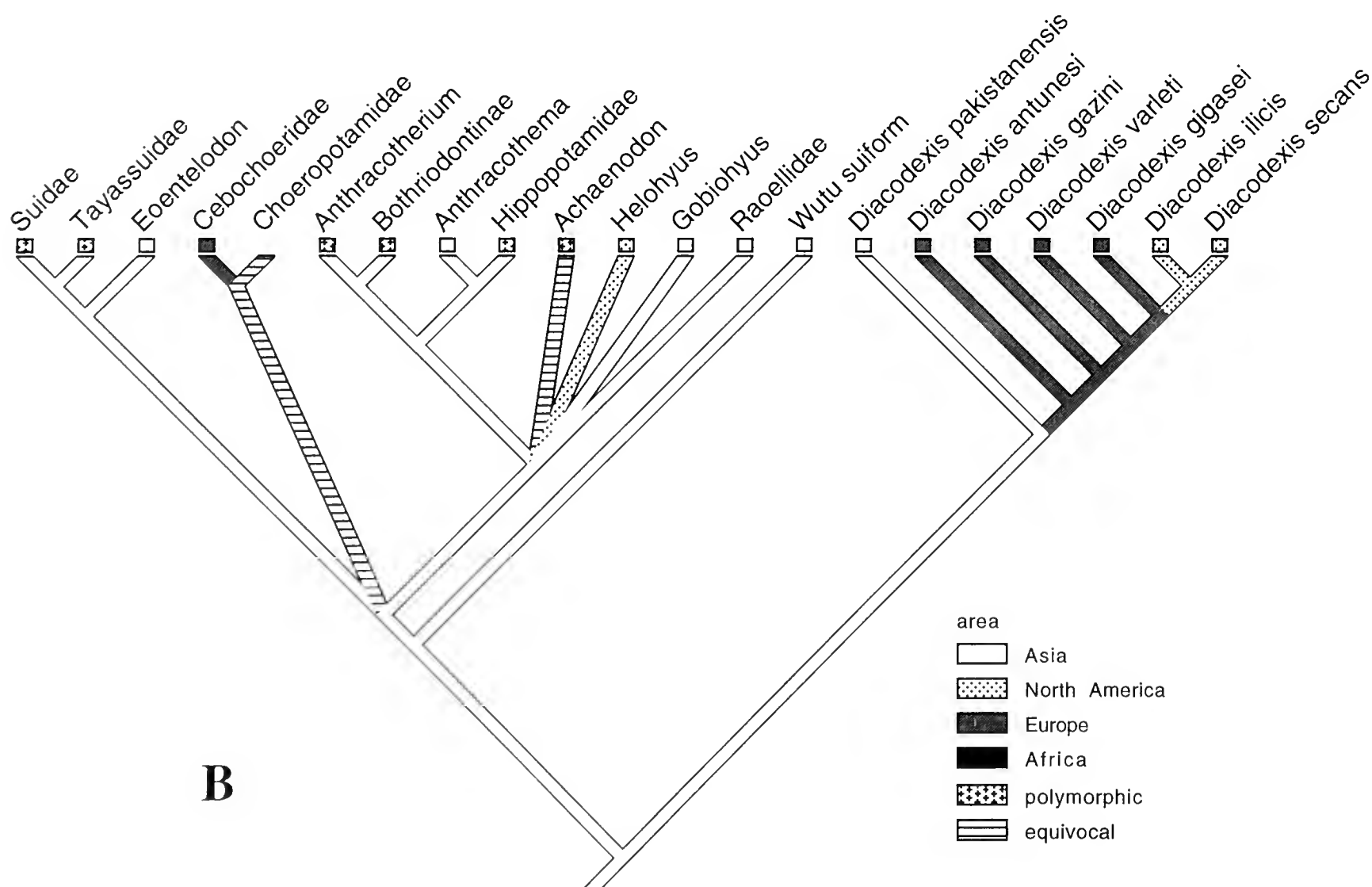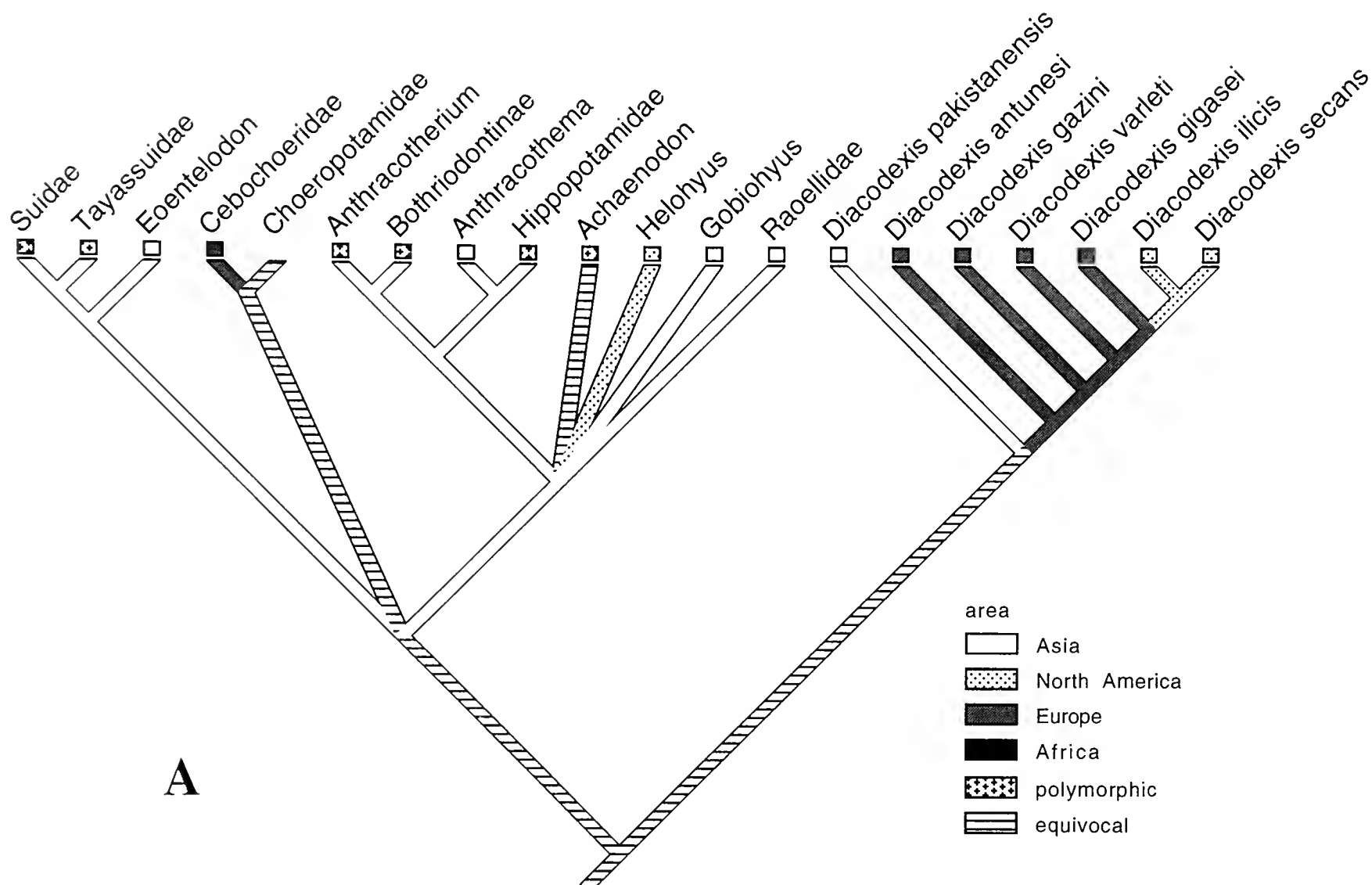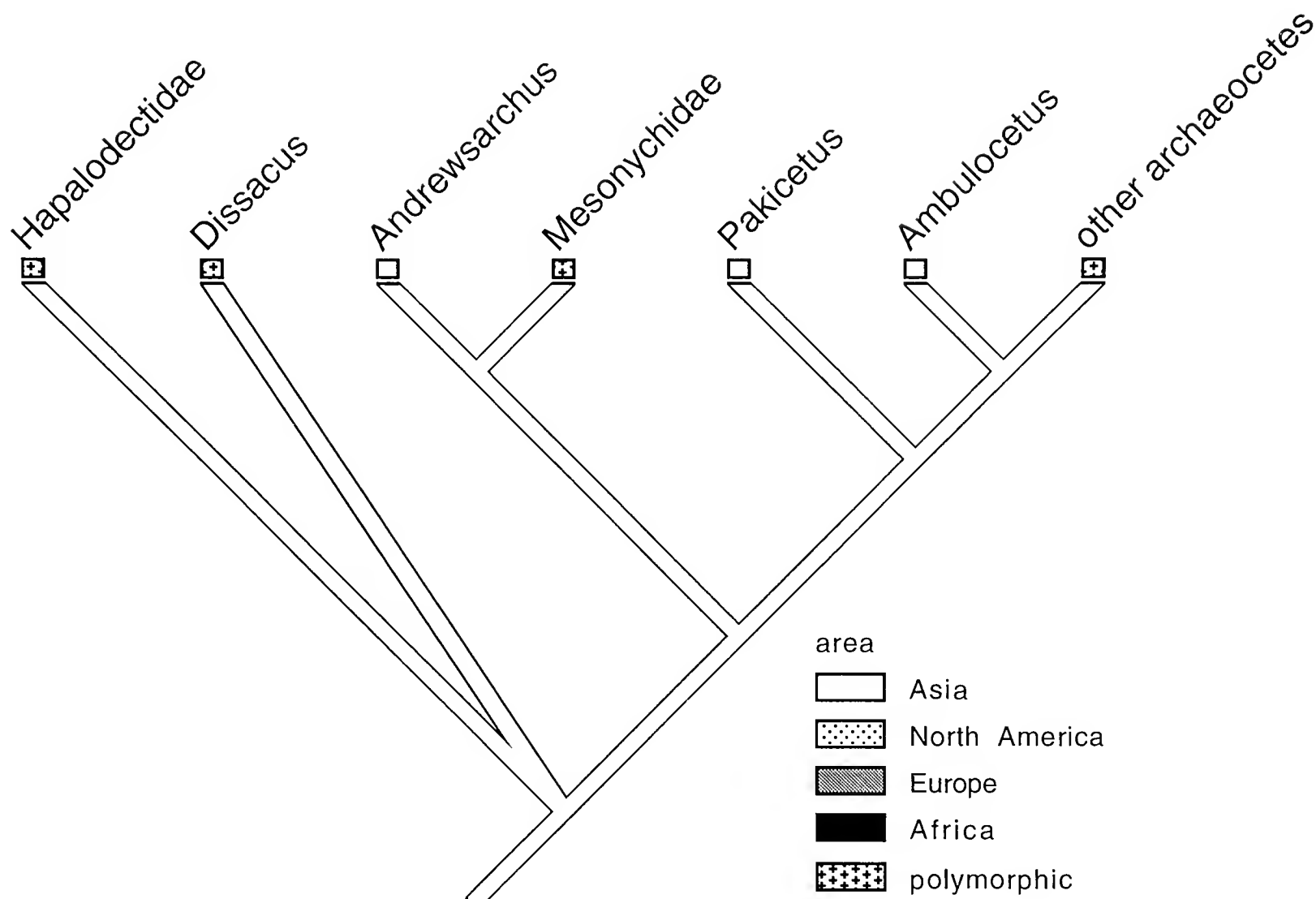
Fig. 5.—A phylogenetically derived biogeographic reconstruction for Cetacea. The tree topology depicted here is based on Thewissen (1994:fig. 4). Note that an Asian origin for Cetacea is unambiguously supported.

worldwide range. However, basal cetaceans show a much more restricted geographic distribution, currently limited to Pakistan and India (Gingerich et al., 1983; Thewissen, 1994; Thewissen et al., 1994, 1996). Accordingly, most modern workers have advocated a geographic origin for Cetacea on the eastern margin of the Tethys Sea, probably near the Indian subcontinent (e.g., Thewissen et al., 1994). Cetacean sister taxa are widely believed to lie within the fossil assemblage often referred to as "mesonychians" (Van Valen, 1966; Gingerich et al., 1983, 1994; Thewissen, 1994), which are well known from all three Holarctic continents.

Thewissen's (1994:fig. 4) phylogenetic reconstruction of basal cetaceans and their relatives provides unambiguous support for the conventional view that cetaceans originated in Asia (Fig. 5). Because such phylogenetically basal taxa as *Pakicetus* and *Ambulocetus* are also the oldest cetaceans currently recognized in the fossil record, this phylogenetically derived biogeographic reconstruction of cetacean origins is consistent with their fossil record. As such, the hypothesis that cetaceans originated near the margin of Tethys in southern Asia can be considered quite robust.

PANTODONTA

Pantodonts are known primarily from Asia and North America, where they are represented in faunas as old as Shanghuan and late Torrejonian, respectively. A single species, *Alcidedorbignya inopinata*, is known from the early Paleocene of Bo-

Fig. 4.—Phylogenetically derived biogeographic reconstructions for Artiodactyla. A. Tree topology based on Smith et al. (1996:fig. 1) for basal neoselenodontians and Gentry and Hooker (1988:fig. 9.8) for suiforms. B. Same topology as A, but with unnamed suiform from Wutu Basin, Shandong Province, China (see Tong and Wang, 1998), inserted as the sister taxon of all other suiforms. Note that with the Wutu suiform excluded from the analysis (A), optimization of the center of origin for the order is ambiguous, with both Europe and Asia being equally parsimonious solutions. If the topology is altered by addition of the Wutu taxon as the most basal member of Suiformes (B), an Asian origin for Artiodactyla is unambiguously supported.
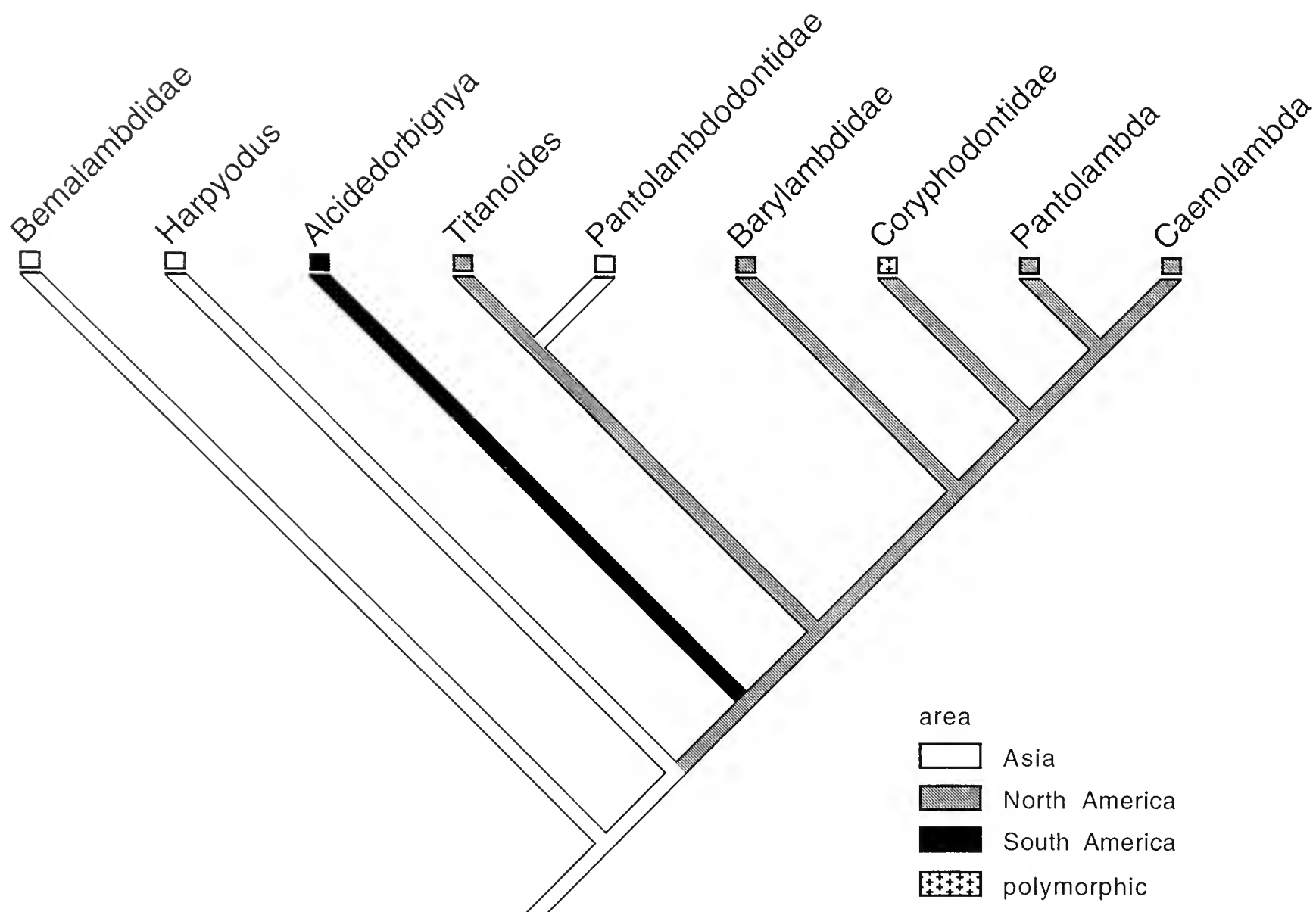
Fig. 6.—A phylogenetically derived biogeographic reconstruction for Pantodonta. Tree topology is based on de Muizon and Marshall (1992) and Lucas (1993). Note that an Asian origin for pantodonts is unambiguously supported. In this case, geographic character states were treated as "ordered," on the assumption that dispersal between Asia and South America must have involved North America as an intermediary.

livia (de Muizon and Marshall, 1992), and several species of *Coryphodon* are recorded from the Sparnacian of western Europe (e.g., Lucas, 1982, 1989). An Asian origin for pantodonts has been supported by several workers (e.g., Chow and Wang, 1979; Krause and Maas, 1990). Alternatively, de Muizon and Marshall (1987) noted that pantodonts may have originated in South America, based on the early record of *Alcidedorbignya* there. Indeed, the early dispersal history of pantodonts is difficult to explain because *Pantolambda*, the earliest pantodont currently recorded in North America (from zone To3), is significantly younger than either the Asian or South American FADs for the order. Presumably, part of the early history of North American pantodonts is yet to be documented in the fossil record, because North America must have served as a corridor for dispersal of early pantodonts between Asia and South America, regardless of where the order originated.

Phylogenetic reconstructions for pantodonts advocated by de Muizon and Marshall (1992) and Lucas (1993) suggest unequivocally that Asia was the continent on which pantodonts originated, because the two basalmost pantodont clades known to date, Bemalambdidae and *Harpyodus*, are restricted to that continent (Fig. 6). The fossil record does not contradict this phylogenetically derived biogeographic reconstruction because the early Shanghuan pantodont records known from the Nanxiong Basin in Guangdong Province, China, are probably roughly coeval with *Alcidedorbignya* in Bolivia (cf. Lucas and Williamson, 1995; Wang et al., 1998).

CORYPHODONTIDAE

The distinctive pantodont family Coryphodontidae is known from many Holarctic faunas (e.g., Lucas, 1984, 1989; Lucas and Tong, 1987; Uhen and Gingerich, 1995), but there is no consensus regarding the continent on which Coryphodontidae origi-
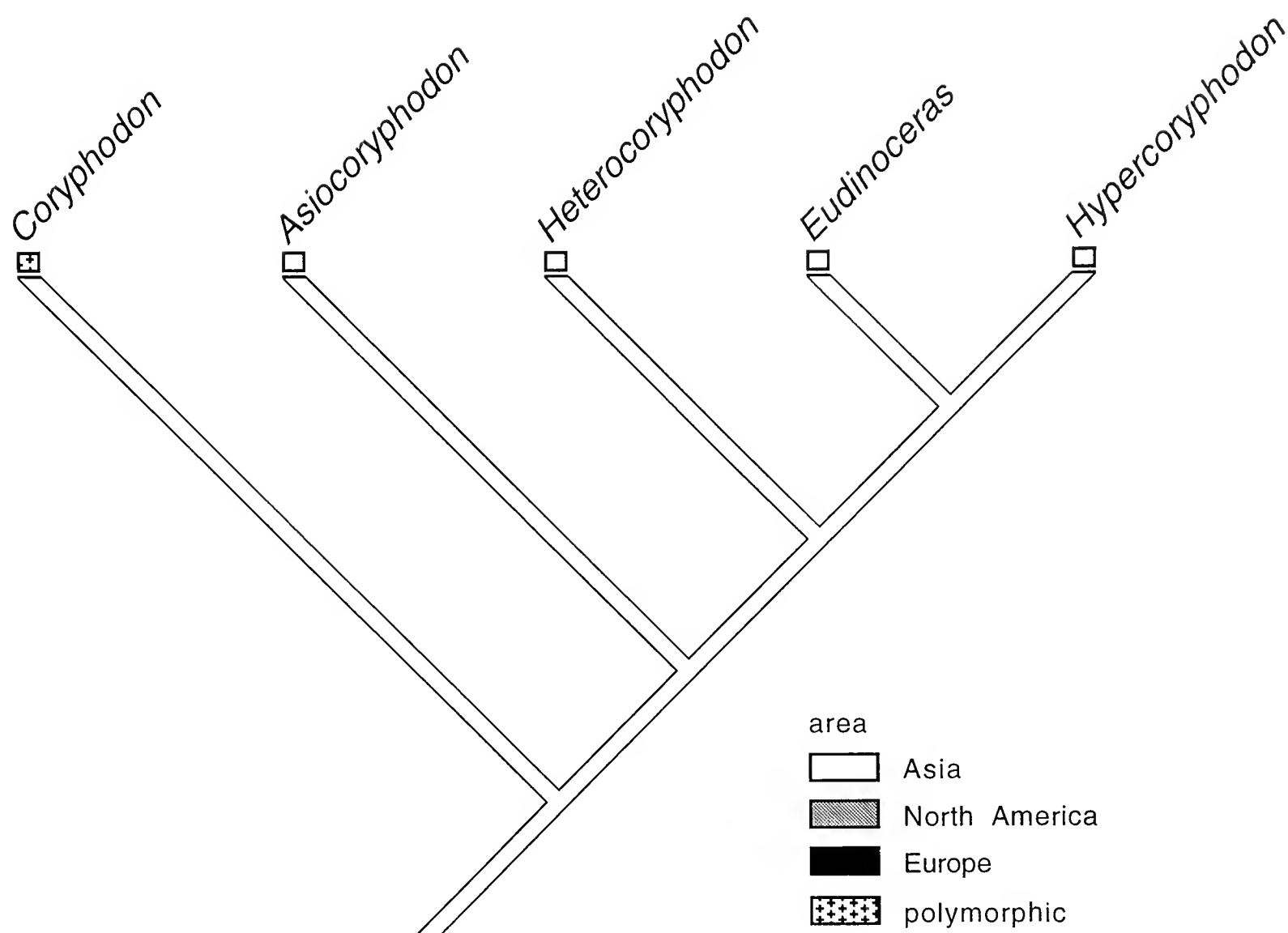
Fig. 7.—A phylogenetically derived biogeographic reconstruction for Coryphodontidae. Tree topology is based on Lucas and Tong (1987:fig. 7). Based on analysis of ingroup relationships among coryphodonts, an Asian origin for the family is unambiguously supported. However, this result conflicts with that shown in Figure 6. See text for further discussion.

nated. Such primitive North American Paleocene pantodonts as *Pantolambda* and *Caenolambda* have been cited as the closest known sister taxa to Coryphodontidae (e.g., Lucas, 1982, 1993), a finding which, if demonstrated to be true, would imply a North American origin for the family (cf. Fig. 6). However, as Krause and Maas (1990:88) recognized, ". . . *Pantolambda* is so primitive relative to *Coryphodon* that the two forms can be allied only indirectly . . . a strictly ancestor–descendant relationship between *Pantolambda* (or *Caenolambda*) and *Coryphodon* is not defensible on present evidence, and no structural intermediates from the fairly well-sampled late Tiffanian of the Western Interior have turned up . . . ." Uhen and Gingerich (1995:284) concurred, noting that "The appearance of *Coryphodon* in the Clarkforkian of North America with no identifiable North American ancestry, suggests that *Coryphodon* may have immigrated from some other continent at this time."

A phylogenetically derived biogeographic reconstruction based on ingroup relationships within Cor-

yphodontidae (Lucas and Tong, 1987:fig. 7) unambiguously points to Asia as the continent of origin for the family (Fig. 7). However, this result conflicts with that shown in Figure 6, in which a North American origin for coryphodontids is favored because of the nested phylogenetic position of coryphodontids as a whole among more primitive North American pantodonts. Because the phylogenetic position of coryphodontids with respect to other pantodonts continues to be debated, an Asian origin for the family (based on Fig. 7) is preferred here. Assessing whether the fossil record of coryphodontids supports or conflicts with an Asian origin for the family is problematic, because of difficulties in establishing intercontinental correlations that are independent of mammalian biostratigraphy during this interval (see below).

Tillodontia

Tillodonts are known from all three Holarctic continents. In North America and Europe, tillodonts first appear relatively late (early Clarkforkian and
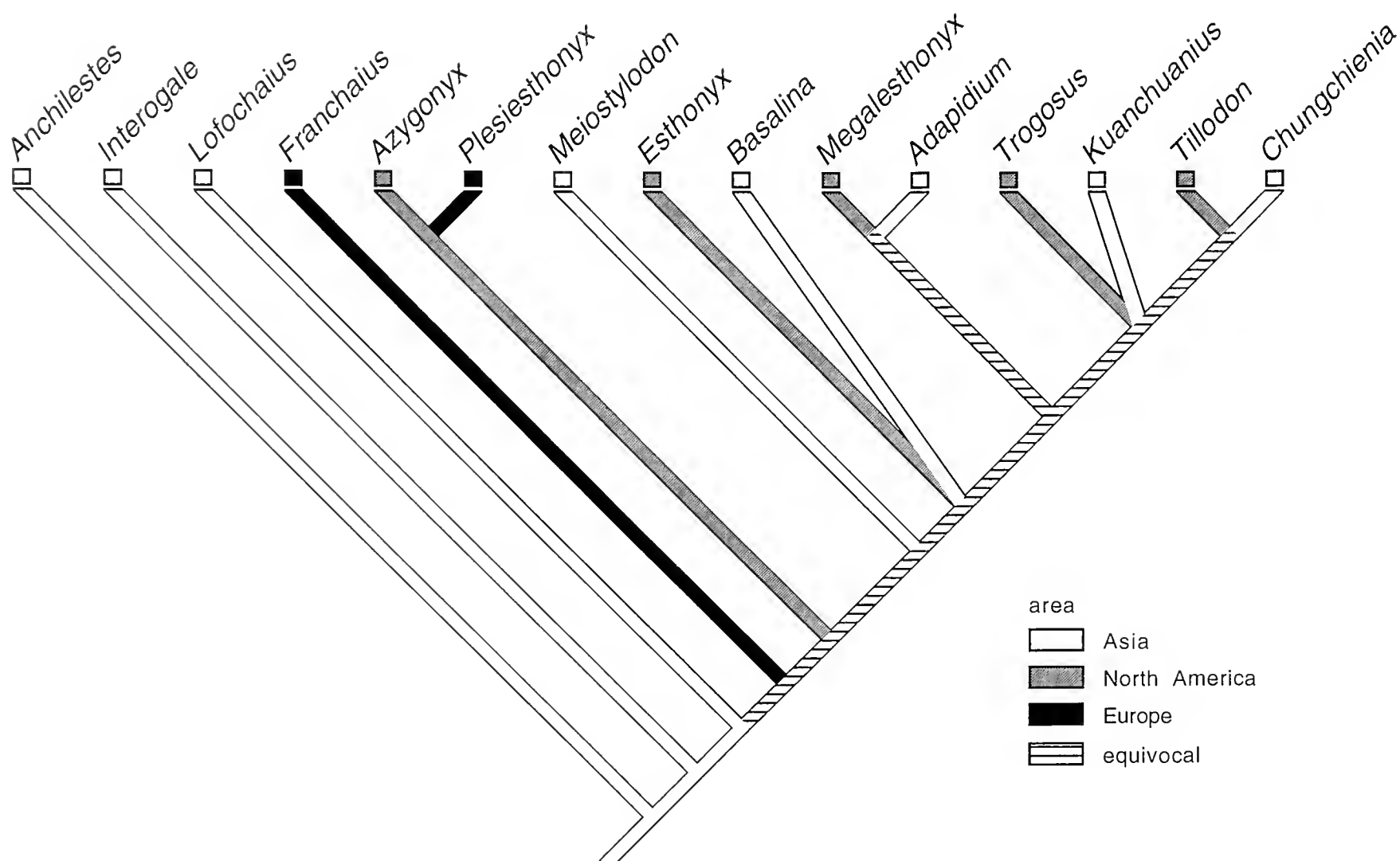
Fig. 8.—A phylogenetically derived biogeographic reconstruction for Tillodontia. Tree topology is based on Gaudry (1992) and Chow et al. (1996:fig. 3B). Note that an Asian origin for tillodonts is unambiguously supported.

Sparnacian, respectively; see Gingerich and Gunnell, 1979; Rose, 1981; Gaudry, 1992), whereas the order is represented in faunas as old as Shanghuan in Asia (e.g., Ting, 1998). Most recent workers acknowledge the likelihood of an Asian origin for tillodonts, given their early fossil record on that continent (e.g., Stucky and Krishtalka, 1983; Ting and Zheng, 1989; Krause and Maas, 1990; Gaudry, 1992; Lucas and Williamson, 1995).

Based on the phylogenetic reconstruction for tillodonts published by Gaudry (1992) and modified by Chow et al. (1996:fig. 3B), an Asian origin for the order is unambiguously favored (Fig. 8). As noted above, the fossil record is clearly in accord with this phylogenetically derived biogeographic reconstruction, such that an Asian origin for tillodonts is a robust biogeographic hypothesis indeed.

DINOCERATA

Undoubted uintatheres are restricted to Asia and North America, where they are recorded in rocks as old as Gashatan and late Tiffanian, respectively (Tong and Lucas, 1982; Schoch and Lucas, 1985; Thewissen and Gingerich, 1987). The South American Paleocene genus *Carodnia* is frequently cited

as a close relative or even as a member of Dinocerata (Simpson, 1935; de Paula Couto, 1952; McKenna, 1980; Gingerich, 1985). Previous hypotheses regarding the continent of origin for Dinocerata have focused on Asia (Schoch and Lucas, 1985) and South America (Gingerich, 1985; Sloan, 1987).

A phylogenetically derived biogeographic reconstruction of the continent of origin for Dinocerata fails to yield an unambiguous result, because both Asia and North America are equally parsimonious optimizations for the node at the base of Dinocerata (Fig. 9). However, no recent worker has seriously considered the possibility that Dinocerata originated in North America, because the order appears suddenly in the North American fossil record during late Tiffanian zone Ti5 and potential sister taxa or close relatives of Dinocerata remain unknown from North America prior to that time. On the other hand, two aspects of the fossil record of early uintathere evolution support an Asian origin for this taxon. First, species of Asian *Prodinoceras* appear to retain certain characters that are more primitive than their counterparts among North American species of *Probathyopsis*. For example, *Prodinoceras* lacks the reduction in size of upper and lower first molars
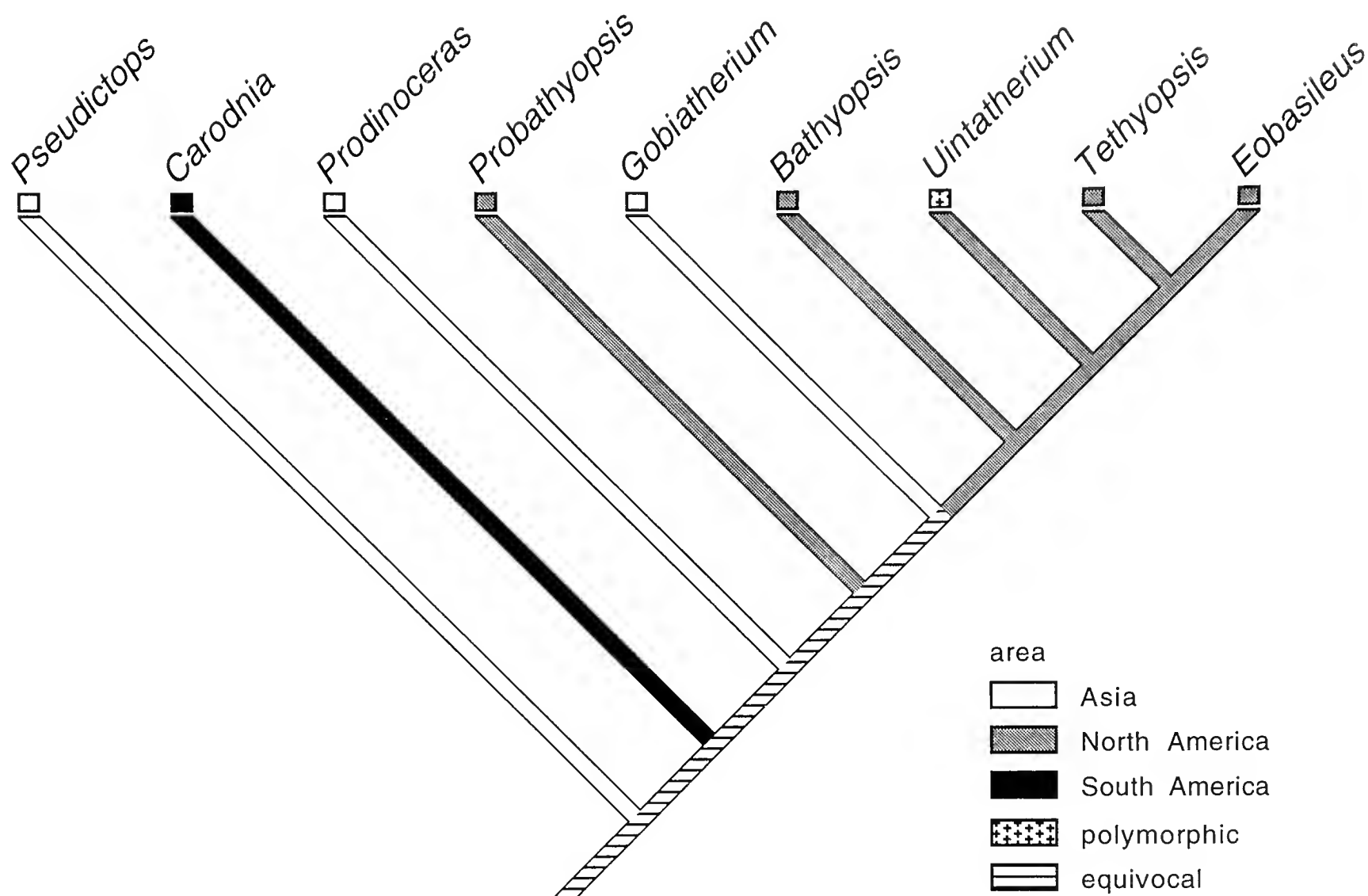
Fig. 9.—A phylogenetically derived biogeographic reconstruction for Dinocerata and their presumed allies. Tree topology is based on Schoch and Lucas (1985:fig. 3), with the addition of North American *Probathyopsis* as a genus distinct from Asian *Prodinoceras*, following Thewissen and Gingerich (1987). As in Figure 6, geographic character states were treated as "ordered," on the assumption that dispersal between Asia and South America must have involved North America as an intermediary. Note that optimization of the center of origin for the order is ambiguous, with both North America and Asia being equally parsimonious solutions.

seen in North American *Probathyopsis* (Thewissen and Gingerich, 1987:fig. 10B). Second, in contrast to the situation in North America, where potential sister taxa for Dinocerata remain unknown, the endemic Asian family Pseudictopidae has been cited as a possible sister taxon of Dinocerata on the basis of dental traits (e.g., Tong and Lucas, 1982; Schoch and Lucas, 1985; Lucas, 1993). If this hypothesis can be corroborated by other data, an Asian origin for Dinocerata would become plausible indeed.

ARCTOSTYLOPIDAE

Arctostylopids are known only from Asia and North America, where the earliest forms occur in faunas of Nongshanian and late Tiffanian age, respectively (Cifelli et al., 1989; Ting, 1998). Traditionally, arctostylopids have been allied with South American notoungulates (for review, see Gingerich, 1985), but thorough study of this issue led Cifelli et al. (1989) to doubt this relationship. In either case, Arctostylopidae appear to represent a valid

clade. Previously, both Asia (e.g., Matthew and Granger, 1925; Cifelli et al., 1989) and North America (by way of a South American notoungulate; see Gingerich, 1985; Sloan, 1987) have been cited as potential centers of origin for arctostylopids.

Based on the phylogenetic reconstruction for Arctostylopidae published by Cifelli et al. (1989:fig. 11), an Asian origin for this clade is strongly preferred (Fig. 10). This phylogenetically derived biogeographic reconstruction agrees with the fossil record of Arctostylopidae in Asia and North America, because the Nongshanian records of early arctostylopids in Asia likely antedate the late Tiffanian FAD for *Arctostylops* in North America (Wang et al., 1998; contra Gingerich, 1985:134–135).

RODENTIA

The most ubiquitous and diverse of all living orders of mammals, rodents today enjoy a virtually worldwide distribution (e.g., Nowak and Paradiso, 1983). While it would thus be difficult to recon-

Fig. 10.—A phylogenetically derived biogeographic reconstruction for Arctostylopidae. Tree topology is based on Cifelli et al. (1989: fig. 11). Note that an Asian origin for arctostylopids is unambiguously supported, with subsequent dispersal to North America of *Arctostylops*.

struct the continent of origin for Rodentia on the basis of neontological evidence alone, consideration of fossil taxa limits the viable options considerably. As a result, no modern worker has seriously considered the possibility of a geographic origin for Rodentia outside of North America and Asia. Indeed, the hypothesis that rodents may have originated in the southern part of North America (Sloan, 1969; Wood, 1977) is now largely discredited. Rather, more recent discoveries of basal rodents and potential rodent sister taxa in Asia make the latter continent a much more plausible candidate for the ancestral rodent homeland (Li, 1977; Li and Ting, 1993; Meng et al., 1994; Tong and Dawson, 1995; Dawson and Beard, 1996).

Phylogenetic relationships among basal rodents and their close relatives as reconstructed by Dawson and Beard (1996) provide unambiguous support for an Asian origin for the order (Fig. 11). This phylogenetically derived biogeographic reconstruction is concordant with the fossil record of early rodents in Asia and North America, although the order Rodentia itself is defined in various ways vis à vis such phylogenetically basal taxa as *Heomys* and Alago-

myidae (Wyss and Meng, 1996). Regardless of such semantic issues, the demonstrably older occurrences of basal rodents (or rodent sister taxa, depending upon one's preferred definition of the order) in Asia corroborate the Asian origin for rodents suggested by phylogenetic data. In particular, the early rodent or rodent sister taxon *Heomys* is known from the Shanghuan of the Qianshan Basin, Anhui Province, China, an interval that is millions of years older than the North American FAD for the order at the beginning of the Clarkforkian (Ting, 1998; Wang et al., 1998). Similarly, the early alagomyid *Tribosphenomys* is known from the Gashatan Bayan Ulan beds of the Erlian Basin, Nei Mongol Autonomous Region, China (Meng et al., 1994, 1998). Although correlation of the Asian Gashatan with the North American sequence of land mammal ages is controversial (see below), Asian *Tribosphenomys* is probably older than the North American early Clarkforkian FAD for rodents (Dawson and Beard, 1996; also see Wang et al., 1998).

ALAGOMYIDAE

First described only recently by Dashzeveg (1990), the basal rodent family (or rodent sister tax-
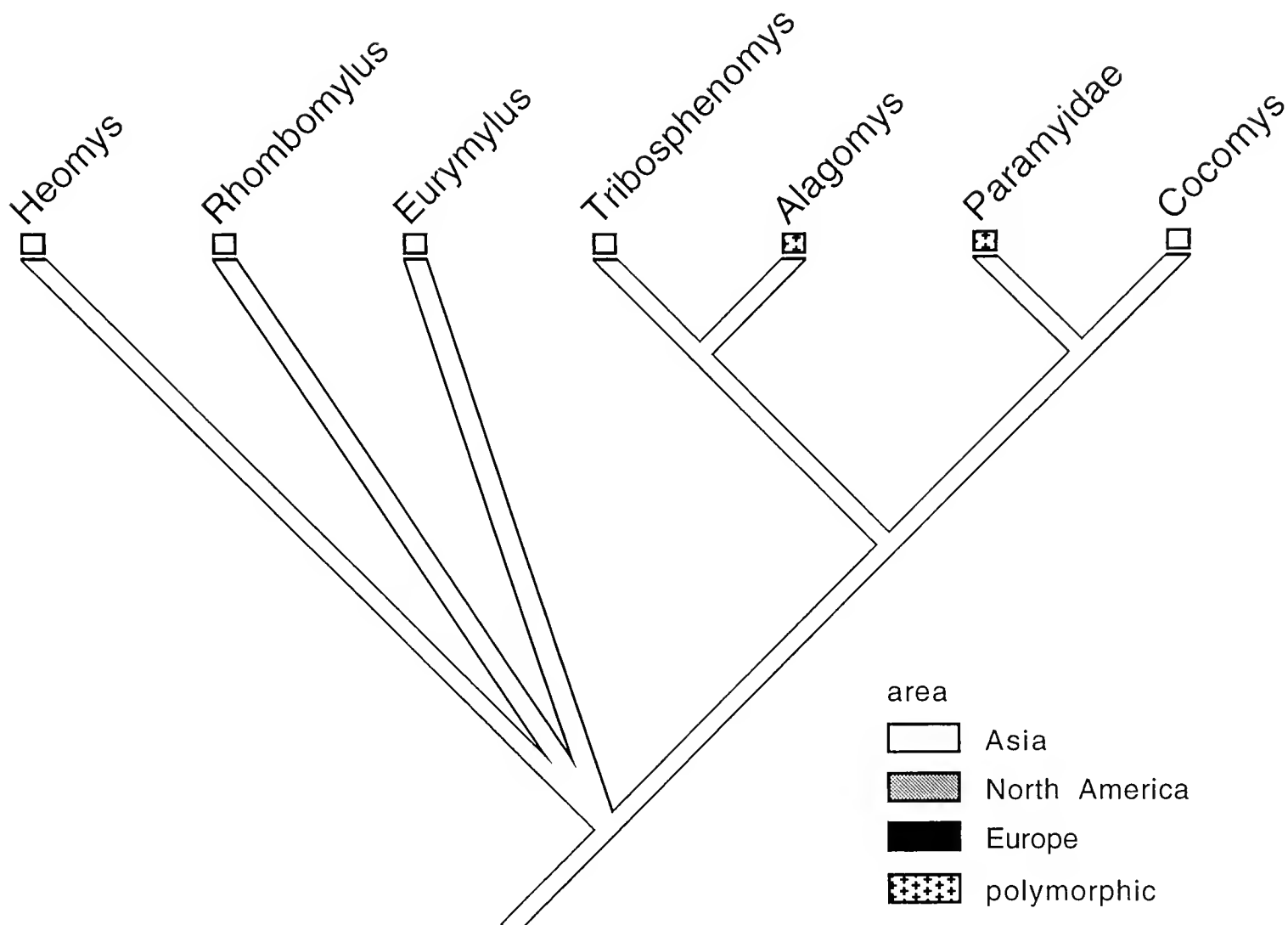
Fig. 11.—A phylogenetically derived biogeographic reconstruction for Rodentia and their presumed allies. Tree topology is based on Dawson and Beard (1996:fig. 1). Note that an Asian origin is unambiguously supported for both the order Rodentia and the family Alagomyidae (*Tribosphenomys* + *Alagomys*).

on; see above) Alagomyidae is now known from the Gashatan Bayan Ulan beds of Nei Mongol Autonomous Region, China (Meng et al., 1994), Bumbanian localities in the Nemegt Basin of southern Mongolia (Dashzeveg, 1990) and the Wutu Basin, Shandong Province, China (Tong and Dawson, 1995), and a single site in North America—the Clarkforkian Big Multi Quarry in the Washakie Basin of southern Wyoming (Dawson and Beard, 1996). Dawson and Beard (1996) attributed the sole North American record of *Alagomys* to immigration from Asia, thereby implying an Asian origin for the family. The possibility that alagomyids originated in North America has never been seriously entertained.

Phylogenetic reconstruction of alagomyids and their close relatives offers clearcut support for the hypothesis that alagomyids originated in Asia, with subsequent dispersal of *Alagomys* to North America (Fig. 11). The fossil record of alagomyids does not contradict this assessment, because the Gashatan record of *Tribosphenomys minutus* in Nei Mongol Autonomous Region, China, probably antedates the

Clarkforkian FAD for Alagomyidae in North America (see above). Interestingly, in Asia *Alagomys* is known only from Bumbanian faunas (Dashzeveg, 1990; Tong and Dawson, 1995), while the sole record of this genus in North America occurs in a Clarkforkian fauna. If alagomyids originated in Asia as is argued here, one would not expect *Alagomys* to occur earlier in North America than in Asia. Accordingly, traditional correlations of the basal Bumbanian in Asia with the basal Wasatchian in North America require reevaluation (see below).

LAGOMORPHA

Despite their nearly cosmopolitan distribution today, lagomorphs have long been considered to have originated in Asia by virtue of their precocious fossil record on that continent (e.g., McKenna, 1982; Li and Ting, 1993). Based on current knowledge of the major features of lagomorph phylogeny (M. R. Dawson, personal communication), a biogeographic reconstruction for Lagomorpha unequivocally supports the traditional hypothesis that lagomorphs originated in Asia (Fig. 12). Because such basal
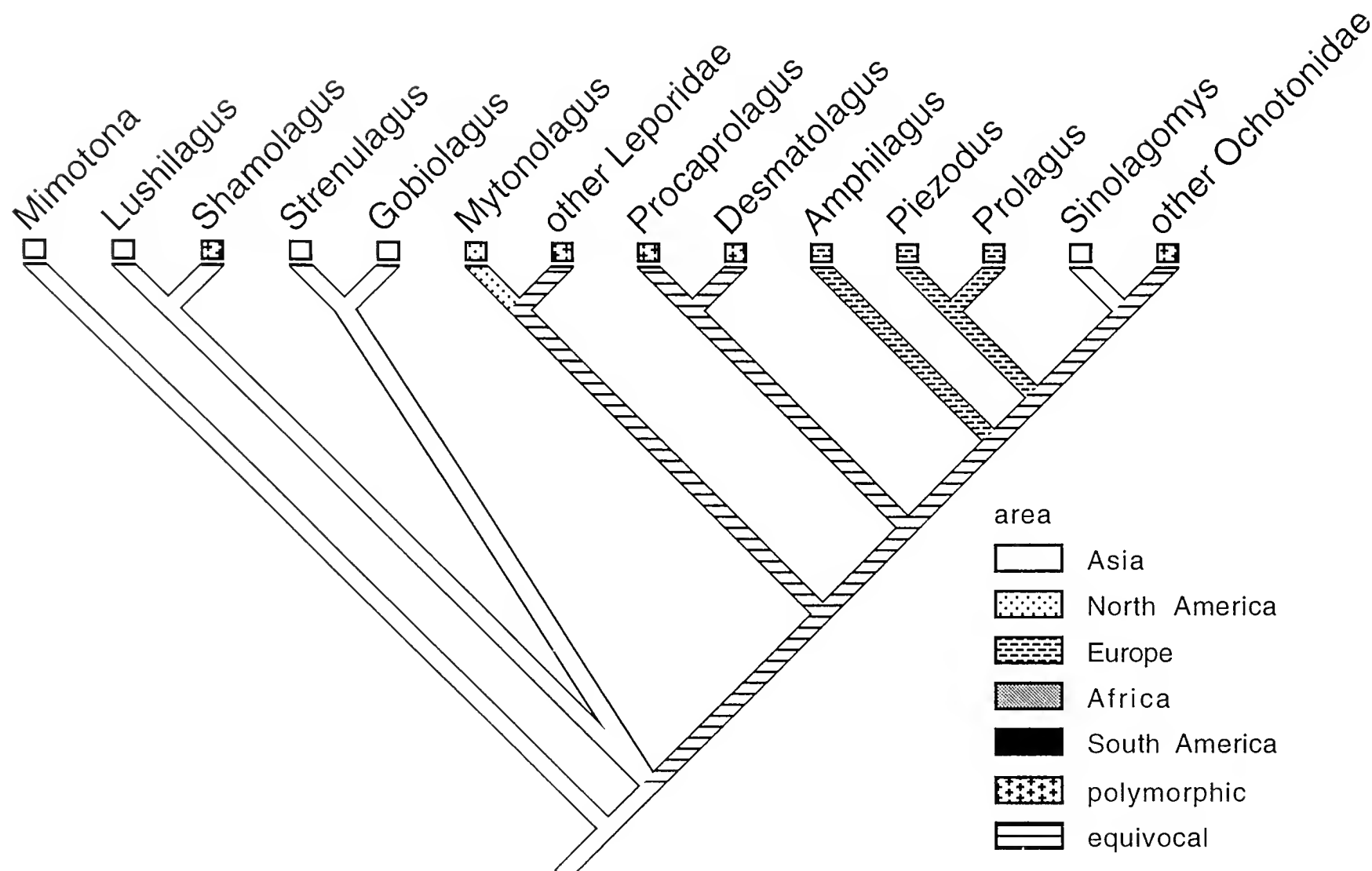
Fig. 12.—A phylogenetically derived biogeographic reconstruction for Lagomorpha. Tree topology is that preferred by M. R. Dawson (personal communication). Note that an Asian origin for lagomorphs is unambiguously supported.

Asian lagomorphs (or lagomorph sister taxa) as *Mimotona* from the Shanghuan and Nongshanian of the Qianshan Basin, Anhui Province, China, are considerably older than the earliest lagomorphs known from other continents, the fossil record of lagomorphs is in complete accord with the phylogenetically derived biogeographic reconstruction shown in Figure 12. Therefore, the hypothesis advocating an Asian origin for Lagomorpha is very strongly corroborated.

PRIMATES

On the three Holarctic continents, undoubted primates (i.e., excluding fossil "plesiadapiforms," see Beard, 1993a, 1993b) are documented as early as the Bumbanian in Asia, the Wasatchian in North America, and the Sparnacian in Europe. According to Dashzeveg (1982, 1988) and Krause and Maas (1990), these FADs on the northern continents may be synchronous (but see below). This pattern of Holarctic occurrences for Primates therefore resembles that known for Perissodactyla and Artiodactyla. The primate *Altiatlasius koulchii* is recorded at the Adrar Mgorn 1 locality in Morroco, which is

thought to be Thanetian in age, making *Altiatlasius* the world's oldest undoubted primate (Sigé et al., 1990). The FAD for Primates in South America is Deseadan (late Oligocene) in age (Kay et al., 1995).

Given the similar pattern of occurrence shown by Primates, Perissodactyla, and Artiodactyla on the Holarctic continents, it is unsurprising that biogeographic reconstructions for these taxa have varied along the same general lines. In particular, early hypotheses advocating an origin for Primates in the southern part of North America (Sloan, 1969; Gingerich, 1976; Schiebout, 1979) have not been corroborated by more recent examination of faunal change across the Clarkforkian–Wasatchian boundary on that continent (Gingerich, 1986, 1989, 1993; Krause and Maas, 1990). As a result, most workers have looked to other continents in searching for the geographical origin of Primates. Discovery of the Thanetian primate *Altiatlasius* in North Africa has strengthened the hypothesis that Primates may have originated on that continent (Gingerich, 1986, 1990; Sigé et al., 1990). Alternatively, Krause and Maas (1990) hypothesized an origin for Primates on the Indian Noah's Ark prior to its collision with Asia.
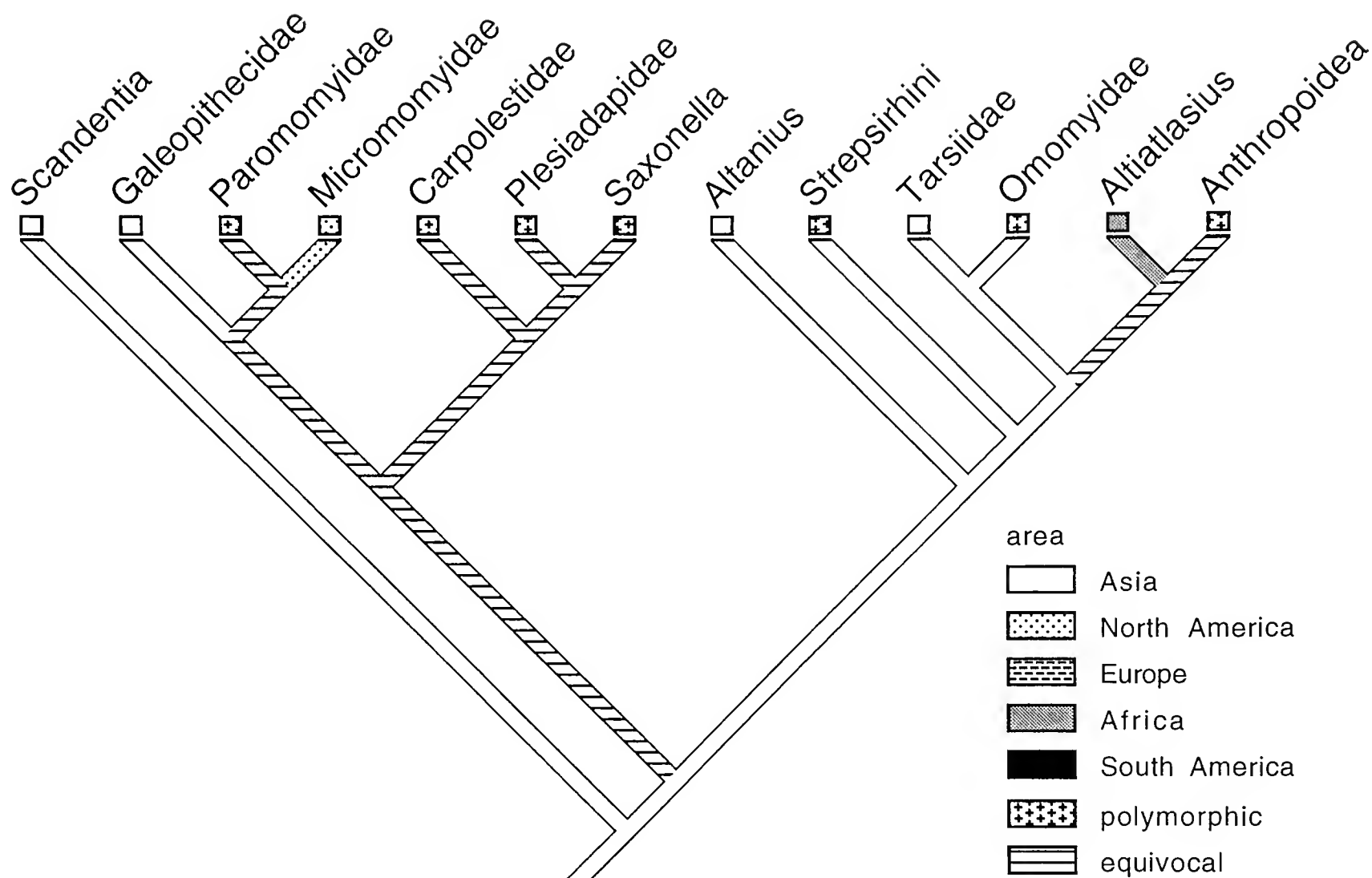
Fig. 13.—A phylogenetically derived biogeographic reconstruction for Primatomorpha + Scandentia. Tree topology is based on Beard (1993*b*) and Beard and Wang (1995) with respect to living and fossil Dermoptera, Gingerich et al. (1991) with respect to *Altanius*, and Beard and MacPhee (1994), Beard et al. (1996), and Beard (1998) for all other primates. Note that an Asian origin for Primates is unambiguously supported.

Finally, based on the poorly known Paleocene taxon *Decoredon anhuiensis* from the Qianshan Basin, Anhui Province, China, Szalay and Li (1986) proposed an Asian origin for Primates. However, the primate affinities of *Decoredon* have been questioned by several workers (Gingerich et al., 1991; Rose and Bown, 1991; Rose et al., 1994; Rose, 1995), so that the earliest record of undoubted primates in Asia remains Bumbanian.

Many details regarding higher-level relationships among primates and their close relatives continue to be vigorously debated. However, my earlier hypothesis advocating the monophyly of a Primates + Dermoptera clade called Primatomorpha (Beard, 1989, 1990, 1991, 1993*a*, 1993*b*) receives continued support here. Molecular phylogenetic studies suggest that Scandentia are closely related to Primatomorpha (e.g., Cronin and Sarich, 1980; Adkins and Honeycutt, 1991, 1993; Ammerman and Hillis, 1992; Bailey et al., 1992; Stanhope et al., 1993), in agreement with the long-standing hypothesis of a close relationship between tree shrews and primates

(e.g., Luckett, 1980; Novacek et al., 1988). Accordingly, Scandentia are accepted as the sister taxon of Primatomorpha here. Relationships among living and fossil dermopterans are based on the work of Beard (1993*b*) and Beard and Wang (1995). Relationships among undoubted primates are reconstructed following the work of Gingerich et al. (1991) for *Altanius* and Beard and MacPhee (1994), Beard et al. (1996), and Beard (1998) for all other taxa.

Based on the phylogenetic relationships depicted in Figure 13, an Asian origin for the order Primates is unequivocally supported. However, this phylogenetically derived biogeographic reconstruction may be in conflict with the primate fossil record as it is currently understood. The Thanetian taxon *Altiatlasius* from Morocco is almost certainly older than the Bumbanian FAD for undoubted primates (in the form of *Altanius orlovi*) in Asia. However, the enigmatic Nongshanian taxon *Petrolemur brevirostre* from the Nanxiong Basin, Guangdong Province, China, was originally described as a pri-

mate by Tong (1979). Although its primate affinities have proven to be controversial (e.g., Szalay and Li, 1986; Rose, 1995), the antiquity of *Petrolemur* is probably similar to that of Moroccan *Altiatlasius*. If *Petrolemur* ultimately proves to be a primate, the Asian origin for Primates supported by the phylogenetic relationships depicted in Figure 13 would be consistent with the fossil record for the order. Otherwise, either the phylogenetically derived biogeographic reconstruction depicted in Figure 13 is flawed or the fossil record of early primates in Asia remains incompletely sampled.

HYAENODONTIDAE

Hyaenodontid creodonts are common carnivorous mammals in Paleogene faunas of North America, Europe, Asia, and Africa. Along with perissodactyls, artiodactyls, and primates, hyaenodontids first occur in North America at the beginning of the Wasatchian. Their FAD in Europe occurs at the beginning of the Sparnacian, which may be synchronous with the North American FAD for this same suite of taxa (Dashzeveg, 1982, 1988; Gingerich, 1989; Krause and Maas, 1990). Important records of early hyaenodontids in Asia are now known from the Gashatan Bayan Ulan fauna of Nei Mongol Autonomous Region, China (Meng et al., 1998), and the Gashatan Naran Member of the Naran Bulak Formation in the Nemegt Basin, southern Mongolia (Dashzeveg, 1988). The earliest hyaenodontid known from Africa is the late early Eocene *Koholia atlasense* from El Kohol, Algeria (Crochet, 1988). Earlier African records of indeterminate hyaenodontids and/or creodonts are based on specimens that are too fragmentary for confident taxonomic allocation (Gheerbrant, 1995).

Previous hypotheses on the area of origin for hyaenodontids have been closely tied to paleobiogeographic reconstructions for the mammal taxa that appear with them at the beginning of the Wasatchian and Sparnacian in North America and Europe, respectively. Because of their sudden appearance in Europe and North America, most workers have argued for an origin of hyaenodontids outside the confines of either of these continents. Two regions in particular, Africa and the Indian subcontinent, have been cited as the most likely areas of origin for Hyaenodontidae. For example, Gingerich (1976, 1989) and Gingerich and Deutsch (1989) argued for an African origin for Hyaenodontidae on the basis of their abundance and diversity in late Paleogene faunas of North Africa. Following the same lines of evidence they marshalled for Perissodactyla, Artiodactyla, and Primates, an origin for hyaenodontids on the Indian subcontinent prior to its collision with Asia was favored by Krause and Maas (1990).

Knowledge of hyaenodontid phylogeny remains sketchy because many taxa are represented by only fragmentary fossils, outgroup relationships are poorly resolved, and a synthetic treatment of the entire clade has yet to be achieved (Polly, 1996). Based on the recent phylogenetic reconstruction of selected hyaenodontids by Polly (1996), identification of the continent of origin for Hyaenodontidae is equivocal (Fig. 14). Both North America and Europe are equally parsimonious optimizations of the basalmost node on the cladogram in Figure 14. However, as noted above, these continents are precisely those that many paleontologists agree are least likely to include the center of origin of hyaenodontids. In either case, this phylogenetically derived biogeographic reconstruction conflicts with the fossil record of early Hyaenodontidae because the world's earliest members of this clade are now known from the Gashatan of central Asia (Meng et al., 1998). Accordingly, either the phylogeny depicted in Figure 14 is incorrect or the early fossil record of hyaenodontid evolution is poorly documented at present. The latter possibility seems likely indeed in the case of Asia, where Bumbanian hyaenodontids have yet to be reported, and Africa, where only the enigmatic taxon *Koholia atlasense* documents the presence of the group prior to the late Paleogene (Crochet, 1988).

EAST OF EDEN: ITERATIVE TRANS-BERINGIAN DISPERSAL AND THE NORTH AMERICAN FOSSIL RECORD

There is a long tradition in paleontology of viewing the North American continent as a vital epicenter of mammalian evolution and diversification. That is, for many years the ancestry of numerous mammalian orders and other higher taxa was sought among older North American mammals (e.g.,

Wood, 1957; Van Valen, 1963, 1971, 1978, 1988; Radinsky, 1966; Sloan, 1969; Gingerich, 1976). This notion pervades a great deal of the literature on early Cenozoic mammal evolution, particularly that before about 1990, although it is frequently difficult to cite specific cases to illustrate the point.
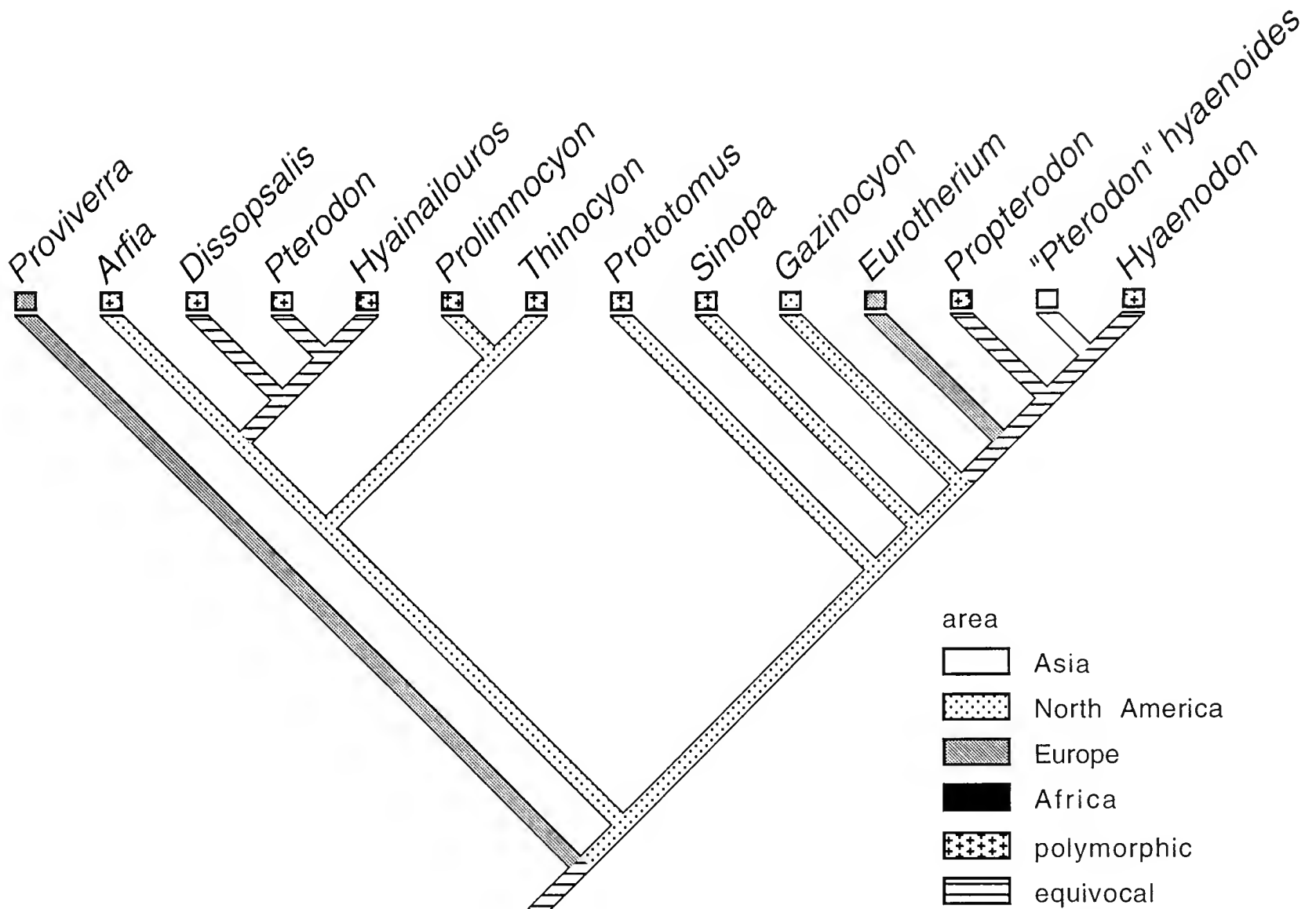
Fig. 14.—A phylogenetically derived biogeographic reconstruction for Hyaenodontidae. Tree topology is based on Polly (1996:fig. 10). Note that optimization of the center of origin for the clade is ambiguous, with both North America and Europe being equally parsimonious solutions. See text for further discussion.

However, Van Valen's (1988:47) statement that "... most mammalian evolution in the Paleocene of North America seems to have been autochthonous" is a revealing example of this general attitude. As knowledge of the phylogeny and biostratigraphy of early Tertiary mammals in North America has improved, the significance of intercontinental dispersal in shaping the North American mammal fauna has come to be increasingly appreciated (e.g., Rose, 1981; Archibald et al., 1987; Krishtalka et al., 1987; Gingerich, 1989; Krause and Maas, 1990; Stucky, 1992; Maas and Krause, 1994; Maas et al., 1995; Woodburne and Swisher, 1995). Nonetheless, ideas regarding the geographic source areas of these mammalian immigrants to North America have been diverse (Krause and Maas, 1990; Woodburne and Swisher, 1995; also see above) and frequently unconstrained by phylogenetic, geophysical, or biostratigraphic data.

In light of the data and interpretations presented above, a new and more cohesive paleobiogeographic model can be presented to account for the dra-matic changes in the North American mammal fauna that are seen throughout much of the early Cenozoic. Under this "East of Eden" model, the vast majority of taxa that appear suddenly in the North American mammal record, with no clear evidence of earlier ancestry on that continent, are viewed as the result of iterative trans-Beringian dispersal from Asia. Highly distinctive taxa that appear suddenly in the fossil record are, by definition, excellent index taxa for purposes of biostratigraphy. As such, the East of Eden model has important implications not only for reconstructing paleobiogeography, but also for biostratigraphic correlation (see next section). Here, I will focus on the East of Eden model as a means of explaining modernization of the North American mammal fauna from the late Tiffanian through the Uintan. Rather than viewing North America as an epicenter of mammalian evolution and anatomical innovation, the East of Eden model treats North America as a biogeographical cul-de-sac that received repeated innoculations of

more "progressive," "modern," or "advanced" taxa from Asia.

Major immigrants to North America during the late Tiffanian include Arctostylopidae and Dinocerata (Archibald et al., 1987; Thewissen and Gingerich, 1987; Cifelli et al., 1989). Based on both phylogenetic and biostratigraphic evidence, the FAD for Arctostylopidae in North America almost certainly resulted from dispersal from Asia (Cifelli et al., 1989; also see above). As noted earlier, phylogenetic and biostratigraphic data currently provide only weak support for an Asian origin for Dinocerata. However, the simultaneous appearance of Dinocerata with Arctostylopidae in North America strengthens the case that uintatheres immigrated from Asia at this time as well.

The onset of the Clarkforkian NALMA (North American Land Mammal Age) is marked by the apparently simultaneous FADs of Rodentia, Tillodontia, and Coryphodontidae (Rose, 1980, 1981; Archibald et al., 1987). Reconstructed phylogenetic relationships and the fossil record agree that an Asian origin for Rodentia and Tillodontia is extremely likely. Paleobiogeographic reconstructions are more ambiguous in the case of Coryphodontidae, but the fact that coryphodontids first appeared in North America in association with two other taxa that are believed to have dispersed from Asia increases the likelihood that coryphodontids followed this route as well.

The beginning of the Wasatchian NALMA is characterized by the simultaneous appearance of Perissodactyla, Artiodactyla, Primates, and Hyaenodontidae—certainly among the more impressive (and vigorously debated) immigration events in the Cenozoic history of North America (Rose, 1981; Gingerich, 1989; Krause and Maas, 1990). Phylogenetically derived biogeographic reconstructions unambiguously support an Asian origin for Perissodactyla and Primates, and an Asian origin for Artiodactyla seems likely as well, depending in part on the phylogenetic position of the Wutu suiform (see above). The fossil record, in the form of the Nongshanian perissodactyl-like taxon *Radinskya yupingae* (McKenna et al., 1989) and the Gashatan hyaenodontid species *Prolimnocyon chowi* (Meng et al., 1998), supports an Asian origin for Perissodactyla and Hyaenodontidae. Similar data are ambiguous in the case of Artiodactyla and Primates because of inadequate controls on intercontinental correlation at this time (see below). Thus, the North American Wasatchian FADs for Perissodactyla, Primates, Artiodactyla, and Hyaenodontidae appear to conform with the East of Eden model in resulting from trans-Beringian dispersal from Asia. The case for an Asian origin for these four mammalian higher taxa is strongest for Perissodactyla (supported by both phylogenetic and biostratigraphic data), less strong for Primates (supported by phylogenetic data; biostratigraphic data are ambiguous at best) and Hyaenodontidae (supported by biostratigraphic data; phylogenetic data do not currently support an Asian origin for this clade), and weakest in the case of Artiodactyla. However, many workers (e.g., Gingerich, 1989:90) have assumed that all four of these taxa must have originated in the same geographic region, following the same route of dispersal. Considering all four taxa at once, the case for an Asian origin is far stronger than that which can be made for any alternative biogeographic reconstruction.

If dispersal from Asia to North America does indeed account for the distinctive reorganization of the North American fauna at the Clarkforkian/Wasatchian boundary, it seems likely on paleogeographic grounds that the same wave of immigrant mammals proceeded at high latitudes across North America to colonize western Europe. A similar paleobiogeographic hypothesis was advanced previously by Gaudry (1992) with respect to tillodonts, which first appear in Europe in the Sparnacian (after the Thanetian hiatus). However, this scenario for the origin of Europe's Sparnacian immigrant mammals runs counter to the biogeographic reconstructions of workers such as Hooker (1980), Godinot (1981, 1982), and Woodburne and Swisher (1995), who advocate dispersal from Europe to North America at this time. For purposes of reconstructing subsequent episodes of intercontinental faunal exchange, it is important to reiterate that rifting in the North Atlantic soon after the basal Wasatchian would have precluded later dispersal directly between North America and Europe (e.g., McKenna, 1983*b*; Stucky, 1992; Woodburne and Swisher, 1995; Ritchie and Hitchen, 1996). This tectonic isolation of North America from Europe virtually requires that all subsequent Paleogene (and most Neogene) immigrant mammals into North America arrived there via a trans-Beringian route, thus ensuring the primacy of the East of Eden model well into the late Cenozoic.

Although the phylogenetic and biostratigraphic data discussed earlier did not treat lower-level perissodactyl taxa, these forms have long played a prominent role in the biostratigraphic subdivision of the Wasatchian (see Gingerich [1991:205–206] for a recent review of this subject), so that some brief

remarks are in order here. Genera of special interest in this context are: 1) the isectolophid *Homogalax*, the FAD of which defines the onset of the Graybullian subage of the Wasatchian (= Wa3) in the usage of Gingerich (1991:table 3); 2) the basal ceratomorph *Heptodon*, the FAD of which defines the beginning of the Lysitean subage of the Wasatchian (= Wa6); and 3) the early brontothere *Lambdotherium*, the FAD of which defines the beginning of the Lostcabinian subage of the Wasatchian (= Wa7; see Krishtalka et al., 1987). Traditionally, these taxa have been viewed as evolving from earlier perissodactyl ancestors in situ in North America. Radinsky (1963:73), for example, thought that *Homogalax* and contemporary *Hyracotherium* are similar enough ". . . that immediate common ancestry seems quite probable." Likewise, *Homogalax* was interpreted by Radinsky (1963) as a stem genus from which the early ceratomorph *Heptodon* was probably derived.

Although this traditional view of autochthonous evolution of Wasatchian perissodactyls in North America cannot be completely refuted at present, the East of Eden model is more consistent with the known data. Trans-Beringian dispersal of *Homogalax* is required in any case, because *Homogalax wutuensis* occurs in the important Bumbanian Wutu fauna of Shandong Province, China (Chow and Li, 1965; Tong and Wang, 1998). Outstanding problems in intercontinental correlation preclude the independent determination of whether or not *Homogalax wutuensis* antedates the North American FAD for the genus (see below). However, Rose's (1996) finding that *Homogalax* retains primitive skeletal characters that have been transformed in *Hyracotherium* seriously weakens Radinsky's (1963) hypothesis of a close common origin between these two genera in North America. Likewise, the phyletic origin of *Heptodon* directly from *Homogalax* is extremely doubtful. More than 35 years of intensive collecting in early Eocene basins in western North America has failed to fill in the morphologic gap acknowledged by Radinsky (1963:75) to separate these genera. Furthermore, in terms of its postcranial skeleton, *Heptodon* seems to resemble *Hyracotherium* more closely than it does *Homogalax* (Rose, 1996). Such primitive Asian ceratomorphs as *Orientolophus hengdongensis* from the Bumbanian Hengdong fauna of Hunan Province, China (Ting, 1993), may represent more promising outgroups for *Heptodon* and its allies than does *Homogalax*. Finally, although it was originally described as a basal chalicothere by Wang (1995), I regard the Bumban-

ian perissodactyl *Danjiangia pingi* from the Yuhuangding Formation, Liguanqiao Basin, Hubei Province, China, as a primitive sister taxon of *Lambdotherium*. The East of Eden model is therefore fully consistent with the stratigraphic pattern of appearance of exotic perissodactyl taxa in North America during the Wasatchian. Indeed, the fact that these perissodactyl genera continue to prove useful in North American Wasatchian biostratigraphy suggests that they immigrated into that continent rather than having evolved in situ there.

Immigrants to North America at the beginning of the Bridgerian include the brontotheres *Palaeosyops* and *Eotitanops* (these genera are sometimes synonymized, but see Mader [1989]), the basal rhinocerotoid *Hyrachyus*, the tillodont *Trogosus*, and suiform artiodactyls in the form of *Helohyus* (Stucky, 1984). All of these taxa are interpreted here as conforming to the East of Eden model. The case for an Asian origin for suiform artiodactyls was discussed above, so that the FAD for this taxon in North America can be easily interpreted as the result of trans-Beringian dispersal. *Trogosus*, like *Megalesthonyx* from the Lostcabinian, possesses a sister taxon in Asia, suggesting multiple, temporally staggered trans-Beringian dispersals of tillodonts near the Wasatchian–Bridgerian boundary (Stucky and Krishtalka, 1983; Chow et al., 1996). The ancestry of the Bridgerian brontotheres *Paleosyops* and *Eotitanops* must be sought outside of North America, where only the autapomorphous *Lambdotherium* is known from earlier rocks. Asian *Danjiangia* is a plausible stem brontothere, suggesting that the broad North American radiation of this family also follows the East of Eden pattern. *Hyrachyus*, like Wasatchian *Homogalax*, is known from both shores of the Pacific (Russell and Zhai, 1987; Prothero et al., 1989), thus indicating trans-Beringian dispersal for this genus in any case.

The onset of the Uintan was defined by Flynn (1986) on the basis of the FAD of Amynodontidae (*Amynodon*). Amynodontids clearly originated in Asia, where both their earliest records (Averianov and Potapova, 1996) and basalmost taxa (Wall, 1989) are known. Certain other mammalian taxa that first appear in North America in the Uintan also can be attributed to trans-Beringian dispersal, and thereby conform to the East of Eden pattern. For example, the earliest North American record of the omomyid primate genus *Macrotarsius* occurs in the Wagonhound Member of the Uinta Formation (Krishtalka, 1978), which is early, but not earliest, Uintan in age (Flynn, 1986). This genus also occurs

in Fissure D at Shanghuang in southern Jiangsu Province, China (Beard et al., 1994), which is thought to be Irdinmanhan in age (Qi and Beard, 1996). The sudden appearance of *Macrotarsius* in North America, coupled with its possibly earlier occurrence in Asia, suggests that *Macrotarsius* may have dispersed into North America from Asia in typical East of Eden fashion.

A number of other mammals first appear in North America more or less synchronously with *Macrotarsius* and likewise appear to conform to the East of Eden pattern. Among these are the oldest undoubted chalicotheres from North America, *Eomoropus* and *Grangeria*, both of which also occur in China (Lucas and Schoch, 1989). Tong and Wang (1998) report fossils pertaining to a Bumbanian chalicothere from the Wutu Basin, Shandong Province, China, a record which, if substantiated, antedates the North American FAD for chalicotheres by millions of years. Otherwise, the oldest and phylogenetically most basal chalicothere currently known is *Litolophus gobiensis* from the Irdinmanhan of Nei Mongol Autonomous Region, China (Radinsky, 1964; Coombs, 1989). Both the alleged chalicothere from Wutu and *Litolophus* suggest an Asian origin for chalicotheres and conformity to the East of Eden pattern for North American *Eomoropus* and *Grangeria*.

Later in the Uintan (Ui2) occurs the North American FAD for the order Lagomorpha. Both phylogenetic and biostratigraphic data agree that lagomorphs originated in Asia (see above; Fig. 12), so that the late Uintan FAD for this order in North America also fits the East of Eden model. A diversity of other mammalian taxa appears for the first time in North America near the FAD for Lagomorpha (Krishtalka et al., 1987; Stucky, 1992; Woodburne and Swisher, 1995), but phylogenetic and biostratigraphic data remain so poorly resolved for these forms that it is premature to judge whether they too conform to the East of Eden biogeographic model.

Although the scope of the preceding discussion has been limited to mammals from the late Tiffanian through the Uintan, there is abundant evidence that the East of Eden model holds for both earlier and later intervals of time and for organisms other than mammals. The North American record of late Cretaceous dinosaurs illustrates the primacy of the East of Eden model during the latest Mesozoic, when ankylosaurids, ceratopsians, hadrosaurine and lambeosaurine hadrosaurs, and tyrannosaurid and troodontid theropods make their first appear-

ances on that continent (Russell, 1993; Sereno, 1997). With regard to these late Cretaceous dinosaurian taxa, Russell (1993:2007) notes that, "By Campanian–Maastrichtian time . . . the western subcontinent [of North America] had received so many groups of Asian dinosaurs . . . and other terrestrial vertebrates that, biogeographically speaking, it effectively merged with Central Asia. During the whole of the Cretaceous, no dinosaurian family is known to have originated in North America." Similarly, certain FADs for North American Paleocene mammals prior to the late Tiffanian may also conform to the East of Eden model. The North American FAD for Pantodonta (in the form of *Pantolambda*) in late Torrejonian zone To3 was identified as the result of dispersal from Asia in the preceding section. Lucas and Williamson (1995) argue for a much more significant episode (or episodes) of East of Eden dispersal near the Puercan–Torrejonian boundary, when they suggest Carnivora (in the form of *Protictis*), Mesonychia (in the form of *Dissacus*), and *Deltatherium* invaded North America from Asia. Of these taxa, perhaps the best case for compliance to the East of Eden model can be made for Mesonychia, because both early and phylogenetically basal mesonychians are known from Asia (Chow et al., 1973, 1977; Lucas and Williamson, 1995). In contrast, the case for an Asian origin for Carnivora was weakened by Fox and Youzwyshyn (1994), who reported fragmentary fossils of the alleged carnivoran *Ravenictis* from the Puercan Ravenscrag Formation, Saskatchewan, Canada. Phylogenetic relationships between North American *Deltatherium* and Asian Paleocene mammals are too poorly documented to permit confident assessment of whether or not conformity to the East of Eden model holds for this taxon. Like *Deltatherium*, a number of mammal taxa appear suddenly in the Paleocene fossil record of North America without having closely related or ancestral forms known from earlier horizons on that continent. These taxa (e.g., Palaeanodonta, Paromomyidae, Carpolestidae, Erinaceidae) too may eventually prove to uphold the dominance of the East of Eden paleobiogeographic model, but evidence remains scant.

Numerous examples of East of Eden dispersal events among mammals subsequent to the Uintan have been reviewed by Woodburne and Swisher (1995). These data demonstrate that Asia has served as a persistent source area for exotic mammalian immigrants to North America throughout the Cenozoic. No other continent has contributed

as many taxa over such an extended interval of time as Asia has to the North American mammal fauna. Future paleobiogeographic studies of plants and nonmammalian vertebrates are necessary to determine the primacy of the East of Eden model for those taxa.

IMPLICATIONS FOR THE BIOSTRATIGRAPHIC CORRELATION OF EARLY TERTIARY MAMMAL AGES OF ASIA

If Asia has indeed served as a biogeographic source area for many of the immigrant mammal taxa that are used for biostratigraphic purposes in North America, the possibility of inferring spuriously young correlations for Asian faunas containing such forms logically follows. For example, because pantodonts are unknown in North America prior to the late Torrejonian (To3), one could argue, as Ting (1998) has, that Shanghuan pantodont records in Asia are unlikely to antedate North American zone To3. However, such a correlation ignores the point that pantodonts, like all clades, must have originated somewhere on the face of the planet (rather than everywhere at once). If pantodonts originated anywhere other than North America, the possibility exists of a significant interval of endemism for pantodonts near the clade's center of origin prior to their dispersal to North America. In fact, given the strong evidence reviewed above that pantodonts originated in Asia, one should actually expect there to be Asian pantodont records that are demonstrably older than To3. Of course, in order to demonstrate an earlier age for at least some Asian pantodonts, an assessment of age that is independent of mammalian biostratigraphy is necessary. Unfortunately, most of the known early Tertiary mammal faunas of Asia are uncalibrated radiometrically (but see Wang et al., 1998), and correlation of Asian mammal faunas to the Geomagnetic Polarity Time Scale remains in its infancy (e.g., Kappelman and Gose, 1995; Xue et al., 1996). In this section the ramifications of the East of Eden model for biostratigraphic correlation of the Gashatan and Bumbanian Asian Land Mammal Ages (ALMAs) are explored. For current views on correlation of the Shanghuan and Nongshanian ALMAs, see Ting (1998) and Wang et al. (1998).

GASHATAN ALMA

The Gashatan ALMA is defined by Ting (1998) on the basis of the first appearance of Rodentia (in the form of the alagomyid *Tribosphenomys*). This definition is less than felicitous because *Tribosphenomys* is currently known from only one of the faunas (the Bayan Ulan fauna of Nei Mongol Au-

tonomous Region, China) that are widely acknowledged to represent the Gashatan ALMA (see Meng et al., 1998; Ting, 1998). Defining the Gashatan on the basis of the first appearance of the more commonly encountered Dinocerata (in the form of *Prodinoceras*) may provide more stability and ease of recognition for this ALMA in the future. In either case, the primary faunas referred to the Gashatan ALMA remain the same: the Bayan Ulan and Nomogen faunas from the Erlian Basin, Nei Mongol Autonomous Region, China; the faunas from the Zhigden and Naran members of the Naran Bulak Formation in the Nemegt Basin, southern Mongolia; and the Gashato fauna from the Ulan Nur Basin, also in southern Mongolia. Additional Chinese Paleocene faunas that may be referred to the Gashatan ALMA include the Taizicun fauna from Xinjiang, the Pinghu fauna from Jiangxi, and the Shuangtasi and Tujinshan faunas from Anhui (Wang et al., 1998).

Opinions regarding correlation of the Gashatan ALMA with the sequence of NALMAs have varied. Meng et al. (1998) and Ting (1998) regard the Gashatan ALMA as essentially correlative with the Clarkforkian NALMA. In contrast, Wang et al. (1998) suggest that the Tiffanian–Clarkforkian boundary lies within the Gashatan, so that the Gashatan is correlative in part with the latter part of the Tiffanian NALMA, although exactly how much of the Tiffanian correlates with the Gashatan was not discussed.

Consideration of the East of Eden model suggests that the correlation of the Gashatan ALMA advocated by Wang et al. (1998) is more likely. Because rodents are among the taxa that appear to have originated and dispersed in East of Eden fashion, the possibility that the FAD for Rodentia in Asia antedates the FAD for Rodentia in North America must be assumed. Indeed, *Tribosphenomys* from the Gashatan ALMA is more primitive than its close relative *Alagomys*, a genus known only from the Bumbanian ALMA and the Clarkforkian NALMA (Dawson and Beard, 1996). Superpositional relationships between Gashatan (below) and Bumbanian (above) faunas are demonstrable in the field in

the Nemegt Basin of southern Mongolia (Dashzeveg, 1982, 1988; Russell and Zhai, 1987). Accordingly, there is every reason to believe that the Gashatan record of *Tribosphenomys* in the Bayan Ulan fauna antedates the Clarkforkian record of *Alagomys* at Big Multi Quarry, Wyoming (Dawson and Beard, 1996). Consideration of Gashatan arctostylopid and dinoceratan records is consistent with this assessment, because both of the latter taxa first appear in North America during late Tiffanian zone Ti5 (Archibald et al., 1987; Thewissen and Gingerich, 1987; Cifelli et al., 1989). Like rodents, arctostylopids appear to have originated and dispersed in conformity with the East of Eden model, such that the earliest Asian records of this clade (which occur in the Nongshanian ALMA) must be expected to antedate zone Ti5, which they seem to do. Therefore, the Gashatan ALMA is regarded here to be partly correlative with approximately the latter half of the Tiffanian NALMA. The Gashatan may also correlate with the early part of the Clarkforkian NALMA, but it seems unlikely that the entire Clarkforkian can be accommodated within the Gashatan.

If the correlation of the Gashatan advocated here is correct, then two records of mammals from the Bayan Ulan fauna of Nei Mongol Autonomous Region, China, become important for determining whether or not the clades they represent also follow the East of Eden pattern. These taxa are the *Lambdotherium*-like perissodactyl and the hyaenodontid *Prolimnocyon chowi* (see Meng et al., 1998). Because both Perissodactyla and Hyaenodontidae first appear at the beginning of the Wastachian/Sparnacian in North America and Europe, their occurrence in an Asian fauna of seemingly greater antiquity supports the hypothesis that both of these clades also conform to the East of Eden model.

BUMBANIAN ALMA

The Bumbanian ALMA is defined by Ting (1998) on the basis of the first appearance of Perissodactyla (in the form of *Orientolophus*). Such a definition seems reasonable, but Ting's (1998) proposed zonation of the Bumbanian, based on perceived evolutionary trends among Asian perissodactyls, is not supported by superpositional relationships observable in the field and may well be overturned by future work. In particular, there is no evidence to support a greater age for Ting's *Orientolophus* Interval Zone than for her *Homogalax* Interval Zone. As such, there is no biostratigraphic basis for inferring that the Wutu fauna (referred to the *Homogalax* Interval Zone) is younger than either the Bumban or Hengdong faunas (both of which are ascribed to the *Orientolophus* Interval Zone). Ting's (1993:205) claim that "The Hengdong specimens [i.e., *Orientolophus*] represent a more primitive ceratomorph than *Homogalax* and *Cardiolophus*" is based on her analysis of dental characters alone, which conflicts with the retention of primitive skeletal traits in *Homogalax* as documented by Rose (1996). Morphological evidence supporting the ceratomorph affinities of *Homogalax* and other isectolophids is weak, and the possibility exists that Isectolophidae comprises the sister group of a much larger clade of perissodactyls (perhaps even all other undoubted perissodactyls).

Virtually all recent workers have considered the Bumbanian ALMA to correlate, in whole or in part, with the North American Wasatchian and the European Sparnacian (e.g., Dashzeveg, 1982, 1988; Krause and Maas, 1990; Ting, 1998). In light of the East of Eden model elaborated above, this correlation likely underestimates the antiquity of at least some Bumbanian mammal faunas, which more likely correlate with the Clarkforkian NALMA.

Phylogenetic and biostratigraphic data supporting an Asian origin for Perissodactyla, Artiodactyla, Primates, and Hyaenodontidae—all of which share North American FADs at the beginning of the Wasatchian NALMA and European FADs at the beginning of the Sparnacian—were reviewed above. If these taxa did indeed originate in Asia, there is no reason to assume that their earliest records on that continent are synchronous with their North American and/or European FADs. Indeed, two of the four taxa (Perissodactyla and Hyaenodontidae) are known from the Gashatan Bayan Ulan fauna (Meng et al., 1998), which is highly unlikely to correlate with North American faunas younger than Clarkforkian (see above). Likewise, phylogenetically derived biogeographic reconstructions unambiguously point to Asia as the center of origin for Primates (Fig. 13) and, less firmly, Artiodactyla (Fig. 4B).

Closer inspection of some Bumbanian records of primates and artiodactyls reveals why correlation with the Clarkforkian NALMA is not so radical as it might appear at first glance. For example, the primate *Altanius orlovi*, from the Bumban Member of the Naran Bulak Formation, has been the subject of considerable debate because it shows anatomical characters that are exceedingly primitive if this taxon is an undoubted primate as opposed to a "plesiadapiform" (Dashzeveg and McKenna, 1977; Rose and Krause, 1984; Gingerich et al., 1991; Rose et al., 1994; Rose, 1995). Gingerich et al.

(1991) reconstructed the phylogenetic position of *Altanius* as comprising the sister group of all other undoubted primates. If this phylogenetic reconstruction is correct, there is no logical requirement for *Altanius* to be as young as North American and/or European primates, all of which would then be nested higher up the primate cladogram. Similarly, the suiform artiodactyl known from the Wutu fauna (see Tong and Wang, 1998) almost certainly lies outside the clade of neoselenodont artiodactyls (including *Diacodexis* spp.) that first appears in North America and Europe at the base of the Wasatchian and Sparnacian, respectively. As such, there is no reason to assume that the Wutu suiform is as young as these more inclusively nested artiodactyls known from Europe and North America.

Perhaps the best case for correlating an Asian Bumbanian fauna with the Clarkforkian NALMA can be made for the diverse mammal fauna being collected from the Wutu Basin in Shandong Province by Tong Yongsheng, Wang Jingwen, and their colleagues (see Tong and Wang, 1998). Several taxa known from Wutu, including the carpolestid plesia-

dapoids *Chronolestes simul* and *Carpocristes oriens* (Beard and Wang, 1995), the alagomyid rodent *Alagomys oriensis* (Tong and Dawson, 1995), and the neoplagiaulacid multituberculate *Mesodmops dawsonae* (Tong and Wang, 1994), suggest correlation with pre-Wasatchian faunas in North America, where carpolestids, alagomyids, and the nearest neoplagiaulacid relatives of *Mesodmops* are unknown from faunas as young as Wasatchian (Archibald et al., 1987; Beard and Wang, 1995; Dawson and Beard, 1996). The only data supporting correlation of the Wutu fauna with the Wasatchian NALMA is the occurrence of artiodactyls and perissodactyls there. As noted above, both of these taxa appear to conform to the East of Eden paleobiogeographic model, and therefore are not adequate grounds for advocating a Wasatchian correlation for the Wutu mammal fauna. Thus, although an independent means of estimating the age of the Wutu mammals is sorely needed, correlation with the Clarkforkian is fully consistent with the entirety of its mammalian fauna, particularly in light of the East of Eden paleobiogeographic model developed here.

DISCUSSION

TEMPO AND MODE OF FAUNAL INTERCHANGE

The East of Eden model holds that, since at least late Cretaceous time, Asia has been a persistently important source area from which new clades have repeatedly dispersed into North America. In North America this iterative pattern of immigration resulted in episodic modernization of its mammalian fauna. Subsequent to the initial rifting of the North Atlantic in the early Eocene, continued faunal links between North America and the Eurasian landmass were only maintained via trans-Beringian dispersal. Moreover, the vast majority of successful trans-Beringian dispersal events occurred in East of Eden fashion, that is, from Asia to North America. What factors account for this repeating pattern of East of Eden dispersal through time, and how does this long-term pattern of faunal interchange between Asia and North America compare with other examples of intermingling of previously separated faunas?

From the late Cretaceous until the Recent, Beringia has always been a potential avenue for dispersal between Asia and North America, at least in the sense that deep marine trenches have never separated what is today the Russian Far East from the

Alaskan mainland (e.g., McKenna, 1983*a*; Worrall, 1991). However, the high-latitude location of this region clearly functioned as a significant filter to dispersal, at least during intervals of cooler climatic conditions. Trans-Beringian dispersal is potentially controlled by three partly interrelated factors: eustatic sea level, regional tectonics, and climate. Data compiled by Woodburne and Swisher (1995) suggest that, at least for the interval encompassing the late Tiffanian through basal Wasatchian, climate may have been the most important of these three variables. A major sea-level lowstand during the middle Tiffanian (TA2.1) witnessed little or no trans-Beringian dispersal, while three closely staggered East of Eden events occurred during the late Tiffanian (Ti5; Dinocerata, Arctostylopidae), basal Clarkforkian (Cf1; Rodentia, Tillodontia, Coryphodontidae), and basal Wasatchian (Wa0; Perissodactyla, Artiodactyla, Primates, Hyaenodontidae), when eustatic sea level was uniformly higher (Woodburne and Swisher, 1995:fig.1). Perhaps, then, the repetitive nature of the East of Eden model derives largely from the fact that dispersal was controlled by climatic fluctuations: whenever climatic conditions allowed Asian endemic taxa to expand their ranges sufficiently northward, nothing pre-

vented them from invading North America. Because the interval from the late Tiffanian through basal Wasatchian was characterized by increasing mean annual temperatures and decreasing latitudinal temperature gradients (e.g., Zachos et al., 1994; Wing et al., 1995), the three episodes of East of Eden dispersal into North America during this interval may have occurred in response to this single sustained warming trend.

By the same token, were it not for the fact that the only potential route for dispersal between Asia and North America is located at such high latitude, interchange between the two continents would likely have been even more extensive and more nearly continuous, preventing the development of significant endemism on either landmass. Dispersal via lower-latitude corridors, such as that between Asia and western Europe at the time of the Grand Coupure and that between North and South America at the time of the Great American Interchange, typically result in broader and more nearly synchronous faunal interchange (e.g., Webb, 1976, 1985; Heissig, 1979; Marshall, 1988; Berggren and Prothero, 1992; Legendre and Hartenberger, 1992).

The strong trend for Asian endemic taxa to colonize North America successfully, but not vice versa, conforms with patterns established during the Grand Coupure and the Great American Interchange. In both of the latter examples taxa hailing from the larger landmass comprised the great majority of successful invaders, while those from the smaller landmass were able to swim against the current much less frequently. Explaining why this pattern should hold—whether because of competitive superiority, MacArthur-Wilson equilibrium theory, or other factors—is debatable (cf. Marshall, 1988), and this subject will not be considered further here.

CLIMATE CHANGE, TIMING OF DISPERSAL, AND
PALEOBIOGEOGRAPHY IN ASIA

The hypothesis that three episodes of East of Eden dispersal spanning late Tiffanian through basal Wasatchian time were caused by a single sustained warming trend was advanced in the previous section. If this hypothesis is accurate, it should be possible to infer something about the paleobiogeographic distributions of the taxa involved in these three closely staggered dispersal events. That is, in light of the prolonged warming trend and the reconstructed pathway of dispersal, it stands to reason that those taxa dispersing first (Dinocerata and Arctostylopidae) ranged into relatively high latitudes within Asia during the early Tertiary. At the same

time, taxa dispersing later (Perissodactyla, Artiodactyla, Primates, Hyaenodontidae) must have been confined to lower latitudes on the Asian landmass. Taxa involved in the intermediate episode of East of Eden dispersal (Rodentia, Tillodontia, and Coryphodontidae) should have ranged farther north than perissodactyls, artiodactyls, primates, and hyaenodontids during the early Tertiary, but not so far north as early in time as uintatheres and arctostylopids. In this way continued warming, or at least further breakdown of latitudinal temperature gradients, would have allowed successive waves of Asian endemic taxa to expand northward until their ranges included the western margin of Beringia, when dispersal to North America became feasible. Timing of dispersal would therefore have been largely a function of climate, which also defined the northern boundaries of taxon ranges.

How does this theoretical model compare with real data regarding taxonomic distributions in the early Tertiary? Unfortunately, nothing is known of the early Tertiary mammals that must have once inhabited the vast region that today comprises the Russian Far East, Alaska, and adjacent parts of northwestern Canada. However, Gashatan faunas of the Mongolian Plateau (the most northerly mammal faunas currently known from the early Tertiary of Asia) are notable for preserving a diversity and abundance of uintatheres and arctostylopids (Dashzeveg, 1982, 1988; Russell and Zhai, 1987; Cifelli et al., 1989; Meng et al., 1998), in agreement with the model's predictions. Also represented at Gashatan localities on the Mongolian Plateau are some of the taxa that dispersed into North America subsequent to the arrival of uintatheres and arctostylopids there. These include alagomyid rodents (Meng et al., 1994, 1998), coryphodontid pantodonts (Dashzeveg, 1982, 1988), a perissodactyl (Meng et al., 1998), and at least one species of Hyaenodontidae (Dashzeveg, 1982, 1988; Meng et al., 1998). Tillodonts, artiodactyls, and primates have yet to be reported from Gashatan localities of the Mongolian Plateau, and earlier Tertiary mammal faunas remain undocumented there. Hence, in the absence of more northerly Gashatan (or earlier) mammal localities on the Asian landmass, it is impossible to test the model's prediction that early uintatheres and arctostylopids ranged to higher latitudes than did contemporary rodents, coryphodontids, perissodactyls, and hyaenodontids. However, the absence of tillodonts in Gashatan localities of the Mongolian Plateau is probably significant paleobiogeographically, because this clade is docu-

mented as early as the Shanghuan in southern China (see above). Primates, artiodactyls, and tillodonts remain unknown in northern China (Shandong Province) and/or the Mongolian Plateau prior to the Bumbanian (Dashzeveg and McKenna, 1977; Tong and Wang, 1998). Interestingly, these three taxa are also undocumented among the high northern-latitude mammal faunas known from the early Tertiary of Ellesmere Island, Canada (Dawson, 1990).

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UNGULATE-LIKE MAMMALS FROM THE LATE CRETACEOUS OF UZBEKISTAN AND A PHYLOGENETIC ANALYSIS OF UNGULATOMORPHA

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ABSTRACT

(Supergrandorder) Ungulatomorpha Archibald, 1996*b* includes (grandorder) Ungulata and (family) "Zhelestidae." "Zhelestidae" Nessov, 1985*a* is best known from the Upper Cretaceous (upper Turonian–Coniacian) Bissekty Formation, Dzhyrakuduk, Kyzylkum Desert, Uzbekistan. Asian taxa (lower Turonian–Coniacian) include: *Kumsuperus avus* Nessov, 1984*b*, nomen dubium; *Zhelestes temirkazyk* Nessov, 1985*a*; *Sorlestes budan* Nessov, 1985*a*; *Aspanlestes aptap* Nessov, 1985*a*; *Sorlestes kara* Nessov, 1993; *Parazhelestes robustus* Nessov, 1993; *P. minor*, n. sp.; and *Eoungulatum kudukensis*, n. gen. and sp. North America taxa (mid-Campanian–early Paleocene) include: *Gallolestes pachymandibularis* Lillegraven, 1976; *G. agujaensis* Cifelli, 1994; *Alostera saskatchewanensis* Fox, 1989; and *Avitotherium utahensis* Cifelli, 1990. European taxa (Campanian–Maastrich-

tian) include: *Lainodon orueetxebarriai* Gheerbrant and Astibia, 1994; *Labes quintanillensis* Sigé *in* Pol et al., 1992; and *Labes garimondi* Sigé *in* Pol et al., 1992. An M_x fragment (late Santonian) from Vinton Bluff, Mississippi, U.S.A., is questionably referred to Ungulatomorpha. *Wania chowi* Wang, 1995 is not a zhelestid but may have anagalidan affinities. "Zhelestids" occur at localities in wetter, low coastal plain settings in western Asia and North America, but are absent from contemporaneous Late Cretaceous sites in higher, drier settings in Mongolia. Diverse Asian "zhelestids" with apomorphies foreshadowing much later archaic ungulates suggest that archaic ungulates reached North America near the end of the Cretaceous via Beringia. A phylogenetic analysis (18 characters of the upper dentition) strongly supports monophyly of Ungulatomorpha, which includes "Zhelestidae" and Ungulata, as represented by the exemplar *Protungulatum donnae*. A close relationship among rodents (represented by *Tribosphenomys*), primatomorphs (represented by *Purgatorius*), and ungulatomorphs is possible, but the resemblances are equally attributable to convergence.

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Резюме. "Суперграндотряд" Ungulatomorpha Archibald 1996b, включает "грандотряд" Ungulata и "семейство" "Zhelestidae". "Zhelestidae" Nessov 1985a лучше всего известно по остаткам из верхнемеловой (поздний турон – коньяк) Биссектинской свиты в Джиракудуке (пустыня Кызылтум, Узбекистан). Азиатские таксоны желестид (ранний турон – коньяк): *Kumsuperus avus* Nessov, 1984b, nomen dubium, *Zhelestes temirkazyk* Nessov, 1985a, *Sorlestes budan* Nessov, 1985a, *Aspanlestes aptap* Nessov, 1985a, *Sorlestes kara* Nessov, 1993, *Parazhelestes robustus* Nessov, 1993, *P. minor* sp. nov., *Eoungulatum kudukensis* gen. et sp. nov. Североамериканские таксоны желестид (средний кампан – ранний палеоцен): *Gallolestes pachymandibularis* Lillegraven, 1976, *G. agujaensis* Cifelli, 1994, *Alostera saskatchewanensis* Fox, 1989, *Avitotherium utahensis* Cifelli, 1990. Европейские таксоны желестид (маастрихт): *Lainodon orueetxebarriai* Gheerbrant et Astiba, 1994 и *Labes quintanillensis* Sige in Pol et al., 1992 (Испания); *Labes garimondi* Sige in Pol et al., 1992 (Франция). Возможно унгулятоморфу

принадлежит фрагмент нижнего моляра из верхнего сантона Винтон Блафф, Миссиссиппи, США. *Wania chowi* Wang, 1995 не является желестидом и возможно родственен анагалидам. "Желестиды" встречаются в местонахождениях на более влажных, низких приморских низменностях, расположенных в западной Азии и Северной Америке, и отсутствуют (или очень редки) в одновозрастных позднемеловых более сухих и выше расположенных местонахождениях в Монголии. Разнообразные азиатские "желестиды" с апоморфиями, предвосхищающими намного более поздние признаки архаичных копытных, достигли Северной Америки ближе к концу мелового периода через Берингию. Филогенетический анализ 18 признаков верхних зубов подтверждает монофилию таксона Ungulatomorpha, который включает "Zhelestidae" и Ungulata (последние представлены *Protungulatum donnae*). Близкие родственные связи между грызунами (представлены *Tribosphenomys*), приматоморфами (представлены *Purgatorius*) и унгулятоморфами возможны, но сходство может быть также объяснено конвергенцией.

INTRODUCTION

For many years the oldest records of archaic ungulates (condylarths) were known from the early Paleocene of North America. Archaic ungulates are the earliest known, primarily herbivorous eutherians and are presumed to include the ancestry of many extinct and extant eutherian orders. The youngest record of this grade of ungulate was thought to be from the middle Miocene (Hoffstetter and Soria, 1986), but a more recent study shows this to be a litoptern (Cifelli and Guerrero Díaz, 1989). The youngest records now appear to be from the early Oligocene of North America (Archibald, in press).

Traditionally, archaic ungulates have been referred to as the order Condylarthra (Cope, 1881). Krause (1984) regarded the order Condylarthra as a grade; McKenna (1987:80) stated that "condylarths" are ". . . a scrap basket of extinct paraphyletic groups," while Prothero et al. (1988:202) claimed that ". . . the 'Condylarthra' is a paraphyletic waste-basket taxon that has long outlived its usefulness, and should be abandoned" (see also Archibald, in press). Prothero et al. (1988) suggested replacing "Condylarthra" with the informal term "archaic ungulate mammals." Use of this new informal term does not solve the problem of deciphering the relationships of early ungulates, but it does discontinue the use of a term that implies, but actually has, no phylogenetic meaning (i.e., it is not monophyletic, or even more precisely holophyletic).

In 1965 Sloan and Van Valen described *Protungulatum donnae* from Bug Creek Anthills, northeastern Montana, U.S.A. This was regarded as the earliest archaic ungulate (Arctocyonidae, ?Oxyclaeninae). At the time of discovery, Bug Creek Anthills was believed to be within the Upper Cretaceous (uppermost Maastrichtian, Lancian) Hell Creek Formation, but more recently is thought to lie within the lower Paleocene (lower Danian, Puercan), Tullock Formation (e.g., Archibald and Lofgren, 1990). Although most or all of the oldest archaic ungulate-bearing sites in eastern Montana are best regarded as earliest Paleocene in age, Fox (1995) has argued that latest Cretaceous (Lancian) archaic ungulates occur in the Upper Cretaceous Frenchman Formation of Saskatchewan, Canada. The age was determined palynologically.

Van Valen (1978) named four more archaic ungulate species which, like *Protungulatum donnae*, were originally thought to occur in the Hell Creek Formation but are now best regarded as coming from the Tullock Formation. These are: *Oxyprimus*

erikseni, *Mimatuta morgoth*, *Protungulatum gorgun*, and *Ragnarok harbichti*. Van Valen (1978) named five additional species from the Tullock Formation, as well as new taxa from various other Paleocene localities, especially the early Paleocene Mantua lentil, Wyoming. Other workers who have described or mentioned latest Maastrichtian and/or earliest Paleocene archaic ungulates from North America include Johnston (1980), Lupton et al. (1980), Archibald (1982, in press), Johnston and Fox (1984), Lillegraven and McKenna (1986), Van Valen (1988), Fox (1989, 1995), Archibald and Lofgren (1990), Luo (1991), and Lofgren (1995).

Until recently, archaic ungulates were unknown from the Late Cretaceous or earliest Paleocene outside of North America. However, in a series of papers de Muizon and Marshall (1987a, 1987b, 1991; de Muizon, 1991) described archaic ungulates from Bolivia, South America, which were first argued to be latest Cretaceous, but are now generally regarded as early Paleocene in age (Van Valen, 1988; Archibald, 1989; Gayet et al., 1991). In 1982 Nessov figured a dentary with heavily worn M_{1-3} from Uzbekistan that he assigned to Eutheria incertae sedis. In 1984(b) he proposed the name *Kumsuperus avus* for the dentary, noting its resemblance to condylarths (archaic ungulates). Butler suggested omnivorous (1989) and herbivorous (1992) tendencies in the dentition of *Kumsuperus*, and later (1990, 1992) regarded it tentatively as an earlier representative of the level of dental development that appears in archaic ungulates and primates. In a series of papers Nessov and his colleagues (1985a, 1985b, 1987, 1993; Nessov and Kielan-Jaworowska, 1991; Nessov et al., 1994; see also Averianov, in press) proposed, figured, and discussed new taxa that were referred to informally as pre-ungulates.

Here, we describe and discuss material from the Bissekty Formation (Upper Cretaceous, upper Turonian–Coniacian, Uzbekistan) that we refer to the apparently paraphyletic family "Zhelestidae," and we compare these fossils with previously described taxa of archaic ungulates. Although clearly related to archaic ungulates known from elsewhere, the western Asian "zhelestids" retain some primitive characters not usually found in archaic ungulates of North America. A new taxon (Ungulatomorpha) was named (Archibald, 1996b) that includes "Zhelestidae" and Ungulata (archaic ungulates or "condylarths" and all other extinct and extant ungulates).

We use the dental terminology shown in Figure 1. Measurements were taken according to the method illustrated by Archibald (1982:fig. 1). Teeth were projected on a computer screen using a video camera mounted on a binocular microscope. Lines drawn on the image using the software MorphoSys version 1.25 (Meacham and Duncan, 1993) run on an AST 486DX/33 computer provided measurements that were rounded to the nearest 0.1 mm. Methods used in phylogenetic analysis are described in that section. Photographs in Figures 11B–F, 12, 14, and 16 are scanning electromicrographs, while those in Figures 7, 9, 11A, 13, 15, 17, 18, and 19 were taken using regular light photography.

Institutional abbreviations are as follows: CCMGE, Chernyshev's Central Museum of Geological Exploration of Saint Petersburg, Russia; IZ-ANUz, Zoological Institute of the Academy of Sciences of Uzbekistan; LACM, Natural History Museum of Los Angeles County; MNA, Museum of Northern Arizona; OMNH, Oklahoma Museum of Natural History; PU, Princeton University (collections now housed at Yale University); UALVP, University of Alberta Laboratory of Vertebrate Paleontology. Material found between 1978–1993 is housed at Chernyshev's Central Museum of Geological Exploration of Saint Petersburg, Russia; material found in 1994 is housed at the Zoological Institute of the Academy of Sciences of Uzbekistan.

PALEOECOLOGICAL, GEOLOGICAL, AND BIOSTRATIGRAPHIC SETTING

Only one specimen of Cretaceous mammal was described from western Asia before 1978. This was the poorly preserved dentary from Kazakstan described as *Beleutinus orlovi* by Bazhanov in 1972. From 1974 through 1994, the first author conducted field work at a variety of sites in western Asia. This included 11 visits to the area of Dzharakuduk in the middle of the Kyzylkum Desert, western Uzbekistan, southeast of the Aral Sea (Fig. 2). He was joined by the second author for the 1994 field season.

Dzharakuduk, which means "well near the escarpment" in Kazak, refers to the small settlement and the well of the same name that lies 2 km southwest of a more than 200 m-high exposure of Upper Cretaceous sediments (Fig. 3). These exposures are the extreme southwestern extension of a much larger topographic and structural high known as the Bukantau Ridge, and they overlook to the southeast a topographic and structural basin called the Mynbulak Depression (Pyatkov et al., 1967).

All but one of the mammalian specimens from western Asia that are discussed in this paper come from a series of localities within the Bissekty Formation (previously referred to as the Taikarshin Beds by Sochava [1968], but see Nessov [1990]), which is approximately in the middle of the Dzharakuduk escarpment (Fig. 2, 3). The Bissekty Formation (Nessov, 1990) consists of 88–103 m of yellowish, cross-stratified, soft sandstones. These are intercalated with thin layers of conglomerates consisting of brown-black pebbles of clay and silt, covered by iron and manganese oxides and hydroxides. Associated paleosols sometimes preserve extensive

clumps of sandstone molds of small tree trunks and *Platanus-*, Lauraceae- and *Viburum*-like leaves (Nessov, 1992:fig. 3). These beds were deposited mainly in brackish water on coastal plains; the fossils are found mostly in the interconnecting brackish, brackish-fresh, and fresh-water channels (Nessov, 1990, 1991, 1992; Nessov and Kielan-Jaworowska, 1991). The "zhelestids" are found only in channel and near-channel deposits of the Bissekty Formation.

The Bissekty Formation fauna includes heterodontid, odontaspidid, mitsukurinid, cretoxyrhinid, and other sharks; polyodontid, acipenserid(?), amiid, lepisosteid, aspidorhynchid, albulid, elopid, and enchodontid actinopterygians; frogs and salamanders including among others, scapherpetontids, batrachosauroidids, albanerpetontids, and gobiatids; adocid, trionychid, chelydrid-like, and other turtles; priscagamid, necrosaurid, teiid-like, scincid-like, and varanid-like lizards; three taxa of crocodilians; azhdarchid pterosaurs; ankylosaurid, hadrosaurid, protoceratopsid?, and ceratopsid ornithischians; sauropods; ornithomimid, therizinosaurid (including segnosaurids [Russell and Dong, 1993]), tyrannosaurid, dromaeosaurid, and avian theropods (Nessov, 1992; Nessov et al., 1994).

Fossil sites or localities at Dzharakuduk can be grouped as occurring in the lower, middle, or upper Bissekty Formation. Those producing "zhelestids" are site CDZH-17a in the lower Bissekty, CBI-4 and 14 in the middle Bissekty, and CBI-5 and 17 in the upper Bissekty Formation (Fig. 4). An entirely Turonian age for the Bissekty Formation cannot be eliminated. It appears more likely, however, that the
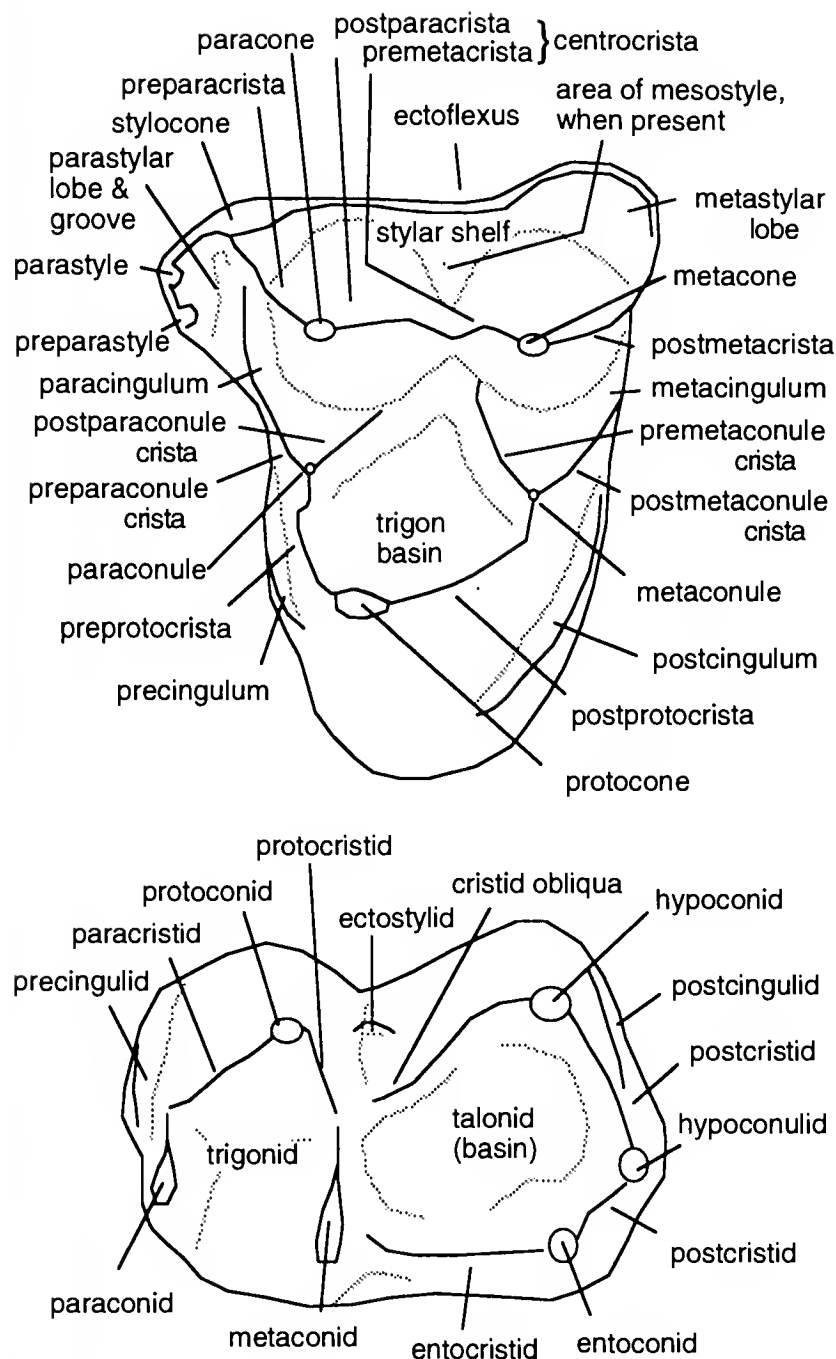
Fig. 1.—Dental terminology modified from Bown and Kraus (1979) and Kielan-Jaworowska and Dashzeveg (1989). Upper molar (top) is based on CCMGE 11/12953, right M^1 (reversed), holotype of *Parazhelestes minor* (Fig. 12B); and lower molar (bottom) is based on CCMGE 13/12953, right M_1 of *Sorlestes budan* (Fig. 15F).

Fig. 2.—Sketch map of the Kyzylkum Desert in western Uzbekistan showing the Dzharakuduk area (2) producing "zhelestids" in relation to other key areas that have been used to assess chronostratigraphic age. These are the same areas shown in the correlation chart in Figure 5 and are as follows: 1, Sultanvais Ridge immediately east of the Amu Dar'ya (Amu River), northwestern Uzbekistan; 2, the Dzharakuduk well area at the extreme southwestern end of the Bukantau Ridge, central Kyzylkum Desert, northwestern Uzbekistan; 3, the Tyulkeli Hill and Zhalmauz well areas in the Dzhalagash region north of the Syr Dar'ya (Syr River), northeastern Aral Sea region, southern Kazakstan; 4, the Fergana region, southwestern Kyrgyzstan.

lower site is late Turonian or possibly even Coniacian in age, while the middle and upper sites are most likely Coniacian.

As shown in Figure 5 the chronostratigraphic age of the Bissekty Formation and its included sites at Dzharakuduk can be established with considerable certainty by means of correlation with other Cretaceous sections in western Asia (a–c in Fig. 5) and by biostratigraphic assessments based on both marine invertebrates and vertebrates (1–11 in Fig. 5).

Nessov and Mertiniene (1986) argued that the middle and upper parts of the Bissekty Formation are Coniacian based on sharks, while the lower part is upper Turonian. This disagrees with Pytakov et al. (1967), who considered the entire unit to be up-

per Turonian. Sochava (1968) and Martinson (1969) regarded this unit as upper Turonian through Santonian. A Santonian age for the mammal-producing levels of the Bissekty Formation is unlikely because the rays from the same levels appear to be older than those of Santonian age of the Fergana depression to the east and the northeastern Aral region to the north.

The Bissekty Formation unconformably overlies a series of marine claystones, shales, and siltstones approximately 90–105 m thick (Abduazimova, 1988) that is argued to be lower Turonian in age (Pyatkov et al., 1967). The upper part of the marine section could be uppermost lower or even upper Turonian (Vereshchagin, 1979). These beds, widespread over Uzbekistan, Kyrgyzstan, Tajikistan, and southern Kazakstan, were deposited during a global transgression in the middle latitudes. They are similar in appearance and lithology to the Mancos Shale and Tropic Shale of North America (Nessov, personal observation), which were deposited under similar conditions during the transgression of a dysoxic sea. In the southwestern Kyzylkum Desert, beds that are stratigraphically equivalent to the low-

Fig. 3.—Exposures in the Dzharakuduk area. View from approximately 2 km east of the settlement of Dzharakuduk, looking toward the northeast. The units are the same as those identified in Figure 4. Distance from the base of the escarpment to the top is about 200 m.

er Turonian of central Kyzylkum (2 in the first column in Fig. 5), yield the early Turonian ammonite *Mammites nodosoides* (Schultz, 1972).

The Bissekty Formation at Dzharakuduk is overlain, sometimes with an angular disconformity of 2–5°, by the 20–61 m-thick Aitym Formation. The Aitym consists of yellowish-gray alternating siltstones and sandstones, overlain by a series of siltstones and sandstones up to 25–40 m thick. The Aitym Formation and overlying Cretaceous siltstones and sandstones contain the teeth of the shark *Hispidaspis* sp., which increases in size toward the upper part of the section. These larger teeth are found in beds referred to the Santonian and Campanian based on marine invertebrates (Sokolov, 1978). Near the top of the Cretaceous part of the section, a transgressive layer of claystones and siltstones contains Campanian marine pelecypods and gastropods. North and east of Dzharakuduk the Campanian is overlain by a thin layer of Maastrichtian sandstones (Abduazimova, 1988); west of Dzharakuduk there are also upper Paleocene marine sandstones with phosphorites (Schultz, 1972).

In the lower part of the Bissekty Formation (26 m above the lower boundary), a channel system yields mammals and other vertebrates (Nessov, 1985*a*, 1987, and references therein), including shark teeth (such as anacoracids). The simple serration and small size of the anacoracid teeth are

typical for late Turonian sharks (Nessov and Mertiniene, 1986). In the middle and upper parts of the Bissekty Formation, channel deposits yield mammals and other vertebrates including shark teeth (e.g., *Ptychocorax aulaticus*). *Ptychocorax aulaticus* (see Kielan-Jaworowska and Nessov, 1990:5) occurs also in Tajikistan and northern Turkmenistan in association with Coniacian marine invertebrates. Ray teeth (e.g., *Myledaphus tritus*) occur in all levels of the Bissekty Formation. In the uppermost part, above the mammal levels, a single *Parapalaeobates*-like ray tooth was found. In other areas of Tajikistan and southern Kazakstan at the Coniacian/Santonian boundary, *Myledaphus* is replaced by a *Parapalaeobates–Baibishia–Protoplathyrina* ray assemblage. The lamnoid sharks that are common in Coniacian brackish water deposits of Uzbekistan become rare in the Santonian of Tajikistan and Kazakstan, where they are replaced almost completely by "orthodonts." The changes in fossil assemblages at the Coniacian/Santonian boundary in the region (c in Fig. 5) also involve other groups of vertebrates, such as lepisosteids, a large species of a mesosuchian crocodile (which disappears at this boundary), sawfish, turtles, theropod dinosaurs, and mammals (Nessov, 1984*b*, 1988, and references therein). The vertebrate assemblage of the Bissekty Formation is similar at the generic and familial level to that in Turonian–Coniacian beds of other regions

of Kazakstan, Uzbekistan, and Kyrgyzstan (with the exception of mammals, which are common in the Bissekty Formation but rare or absent in rocks of similar age in neighboring countries).

In the September 1994 field season at Dzharakuduk, Oleg Tsaruk (Zoological Institute of the Academy of Sciences of Uzbekistan), found a small (~8 cm diameter), well-preserved ammonite near the top of the Dzharakuduk escarpment in an unnamed unit (Fig. 4). A. A. Atabekijan (Russian Geological Institute) identified it as *Placenticeras kysylkumense*, which is characteristic of the Santon-

ian (1994, personal communication to first author). The highest vertebrate sites in the Bissekty occur 100 m below the level at which this Santonian ammonite was found.

Thus, it is likely that most, if not all of the Bissekty Formation is Coniacian in age. The lower Bissekty could be uppermost Turonian, as the contact with the underlying, thick marine units is erosional and the Turonian/Coniacian boundary is not found in these marine units, which perhaps encompass most of the Turonian (Fig. 4, 5).

SYSTEMATIC PALEONTOLOGY

(Class) Mammalia Linnaeus, 1758
(Subclass) Trechnotheria McKenna, 1975
(Infraclass) Cladotheria McKenna, 1975
(Legion) Theria, Parker and Haswell, 1897
(Supercohort) Placentalia Owen, 1837
(Cohort) Epitheria McKenna, 1975
(Superorder) Preptotheria McKenna, 1975
(Supergrandorder) Ungulatomorpha, Archibald,
1996*b*

Included Taxa.—(Family) "Zhelestidae" and (grandorder) Ungulata (taxa included within Ungulata are listed under the rediagnosis for this taxon).

Distribution.—(Family) "Zhelestidae": Late Cretaceous of Asia, North America, and Europe; early Paleocene of North America. Ungulata: Late Cretaceous(?)–Recent of North America; late Paleocene–Recent of Europe; early Paleocene–Recent of South America; early or middle Paleocene–Recent of Asia; middle Eocene–Recent of Africa; early Eocene–Recent, most oceans and some rivers.

Definition.—(As in Archibald, 1996*b*) The most recent common ancestor of "Zhelestidae" and Ungulata and all of its descendants. This is a node-based phylogenetic definition following the protocol suggested by de Queiroz and Gauthier (1990).

Diagnosis.—(Expanded and modified from Archibald, 1996*b*). Those character states labeled with a dagger (†) appear to be apomorphic for Ungulatomorpha while those not so labeled appear to be plesiomorphic or their polarity cannot be determined. Differs from other Late Cretaceous eutherian mammals (including earliest anagalidans) and earliest primatomorphs (i.e., *Purgatorius*) in the following: protocone anteroposteriorly expanded, if only slightly (some expansion also in *Paranyctoides*); upper molar crown in occlusal view at most

only slightly constricted through conular region; parastylar region with two cuspules in earliest diverging taxa (also in *Kennalestes* and *Sailestes*), reduced to one or none in later taxa; paracone/metacone and protocone relatively far apart in earlier diverging taxa (in later diverging taxa protocone migrates labially), with conules closer to paracone/metacone; paraconid lingual to sublingual with some appression to metaconid (†); entoconid and hypoconulid twinned (†) (also in some zalambdalestids). Differs from other Late Cretaceous eutherian mammals (including earliest anagalidans) but shares with earliest primatomorphs (i.e., *Purgatorius*): molar crown shape in occlusal view trapezoidal (also *Paranyctoides*), subrectangular, or rectangular, but not triangular; trigonid height lower relative to talonid height (†); talonid expanded to same or greater width than trigonid (†). Differs from most other Late Cretaceous eutherian mammals (including earliest anagalidans) but shares with *Gypsonictops*, the earliest primatomorphs (i.e., *Purgatorius*), and some later anagalidans (e.g., the rodent *Tribosphenomys*) a stylar shelf that is narrow (†) (possibly also *Barunlestes*). Shares with *Gypsonictops, Asioryctes, Batodon, Kennalestes,* and *Paranyctoides* pre- and postcingula consistently present, but differs from these taxa and is (convergently?) like *Purgatorius* and *Tribosphenomys* in having pre- and postcingula that reach or extend below the conules (†). Shares with *Sailestes, Zalambdalestes, Gypsonictops, Purgatorius,* and *Tribosphenomys* paracone and metacone of similar height. Shares with *Kennalestes, Zalambdalestes, Gypsonictops, Purgatorius,* and *Tribosphenomys* ultimate upper premolar has metacone or swelling (metaconid or swelling on lower). Shares with *Paranyctoides, Otlestes, Sailestes, Zalambdalestes, Gypsonictops, Purgatorius,*

and *Tribosphenomys* paracone and metacone with separate base.

Discussion.—We include in Ungulatomorpha the Late Cretaceous species of ungulate-like mammals from Asia, Europe, and North America ("Zhelestidae") plus (the grandorder) Ungulata, which includes all later archaic ungulates and ungulates. A rediagnosis and discussion of Ungulata follow a description of the "zhelestids."

Soon after the Cretaceous/Tertiary boundary, archaic ungulates began a tremendous morphological and taxonomic radiation leading to the great diversity we see today in ungulates, sub-ungulates, and whales. If our systematic hypotheses are even broadly correct, the above diagnostic characters were very quickly modified as ungulates began to radiate, leaving us with no dental synapomorphies with which to unite extant ungulates.

We presented an exhaustively detailed formal taxonomy at the beginning of this section. This was to provide a phylogenetic framework for understanding where we place Ungulatomorpha. The additional categories (ranks) and taxa are those used by McKenna (*in* Stucky and McKenna, 1993). We do not agree among ourselves as to the merits and need to use categories (ranks), but they have been provided in parentheses for those who wish them. Rather than invent a wholly new categorical name for Ungulatomorpha, however, we simply modified an existing category by adding the prefix "super" to "grandorder" to signify its greater inclusivity.

(Family) "Zhelestidae" Nessov, 1985*a*

As Nessov et al. (1994) noted, Zhelestinae Nessov, 1985*a* was proposed for *Zhelestes temirkazyk*, which is based on an upper dentition. In 1990 Nessov raised this to Zhelestidae. In his 1985(*a*) paper Nessov also erected the taxon Mixotheridia (including Zhelestidae) as a suborder with phylogenetic ties to Scandentia. As originally conceived, Mixotheridia included taxa based on lower dentitions: *Gallolestes*, *Sorlestes*, *Taslestes*, and *Aspanlestes*. With subsequent field work by the first author in the Kyzylkum Desert of Uzbekistan (Nessov et al., 1994), it became clear that zhelestids represented the upper dentitions of mixotheridians.

Our analysis, confirming early suggestions (e.g., Butler, 1990; Nessov, 1993), shows that among the named Late Cretaceous eutherians, there is a group based on both upper and lower dentitions that has phylogenetic affinities to ungulates, notably the early Tertiary archaic ungulates. Using the synapomorphies in the preceding diagnosis, we unite these
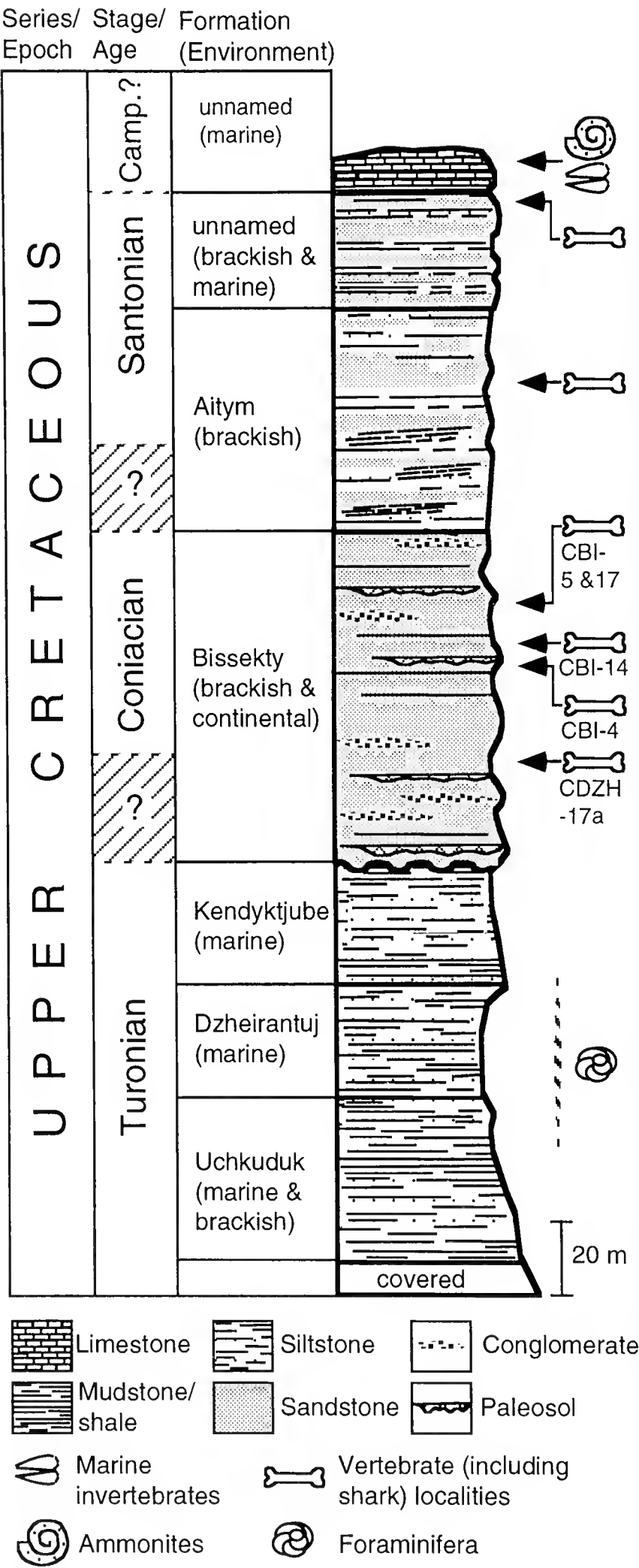

Fig. 4.—Geological section in the Dzharakuduk area. Stratigraphic occurrence of vertebrate localities is shown to the right of the section, as are occurrences of other fossils discussed in the text and in the caption of Figure 5.

Uzbek species, along with species from Kazakstan, North America, and Europe, with Ungulata (sensu stricto) in (the supergrandorder) Ungulatomorpha. The species are as follows: Uzbek species: *Zhelestes temirkazyk* Nessov, 1985a; *Sorlestes budan* Nessov, 1985a; *Aspanlestes aptap* Nessov, 1985a (including *Zhelestes bezelgen* Nessov, 1993); *Parazhelestes robustus* Nessov, 1993; *Parazhelestes minor* n. sp.; *Eoungulatum kudukensis* n. gen. and sp.; and *Kumsuperus avus* Nessov, 1984b, nomen dubium; the Kazak species *Sorlestes kara* Nessov, 1993; and the North American species *Avitotherium utahensis* Cifelli, 1990; *Alostera saskatchewanensis* Fox, 1989; *Gallolestes pachymandibularis* Lillegraven, 1976; and *G. aguajensis* Cifelli, 1994; *Lainodon orueetxebarriai* Gheerbrant and Astibia, 1994 and *Labes quintanillensis* Sigé *in* Pol et al., 1992, from Spain; and *Labes garimondi* Sigé *in* Pol et al., 1992 from France. Questionably included is: the fragmentary M_1 or M_2 from Vinton Bluff, Mississippi, U.S.A., described by Emry et al. (1981).

Other taxa, such as *Taslestes*, do not appear to belong to the ungulatomorph clade and are accordingly excluded. We also remove "zhelestids" from Mixotheridia.

Further, we detected no apomorphies that clearly link all Uzbek ungulatomorphs into a clade that is, in turn, the sister taxon to Ungulata (sensu stricto). This means that Zhelestidae is paraphyletic and is indicated as such by double quotation marks. We retain "Zhelestidae" as a convenient name to use when referring to these Asian, European, and North American ungulatomorphs.

"Zhelestids" do share character states with one another; however, as will be shown in our phylogenetic analysis, these are either primitive retentions of Late Cretaceous eutherians or are also shared with later ungulates. The characters states shared by "zhelestids" and ungulates are those given in the diagnosis of Ungulatomorpha. These are not regarded as synapomorphies of "zhelestid" species.

There are some character states seen in "zhelestids" as well as in a variety of other Late Cretaceous eutherians (see Table 4). This strengthens our view that these states are primitive for some earlier node within Eutheria, if not for the taxon as a whole. The primitive character states that "zhelestids" share with some or all other Late Cretaceous eutherians are: well-developed postparaconular and premetaconular cristae on the upper molars; metacingulum formed of only the postmetaconule crista, while the metacrista runs from the apex of the metacone to the metastylar region (also in some Paleocene taxa

such as *Purgatorius*); a definite parastylar lobe; five teeth present (at the same time) between the canine and the molars in the maxilla and dentary; a metacone or similar swelling on the ultimate upper premolar (which we call P^5), and a metaconid or similar swelling on the ultimate lower premolar (which we call P_5). The last two character states could be primitive retentions; otherwise they evolved convergently among Late Cretaceous eutherians.

Although five teeth present (at the same time) between the canine and the molars in the maxilla and dentary have not been demonstrated in most "zhelestids," they are present or represented by alveoli in *Zhelestes temirkazyk* and *Sorlestes budan*, which may be conspecific (see Fig. 10), and in a larger "zhelestid" (see Fig. 19A–C.) We identify these teeth as P^1_1 through P^5_5 mostly for convenience, although we have no clear basis to argue that all five positions are second generation or successional premolars. Other Late Cretaceous eutherians that possess five teeth at the same time (sometimes based only on alveoli) between the canine and the molars in the maxilla and/or dentary in some individuals are *Gypsonictops hypoconus* (Clemens, 1973), *G. illuminatus* (Lillegraven, 1969), *Kennalestes gobiensis* Kielan-Jaworowska (1981), and *Otlestes meiman* (Nessov, 1985a). In addition, Kielan-Jaworowska and Dashzeveg (1989) reported five premolars in Early Cretaceous *Prokennalestes trofimovi* and *P. minor*.

Unlike *Gypsonictops* and "zhelestids," in which P^3 and P_3 are distinctly smaller than immediately adjacent teeth, in *Kennalestes*, *Otlestes*, and *Prokennalestes* P^3_3 (also referred to as Px or Pc in *Kennalestes*) is not a distinctly smaller tooth. Also, in taxa in which it is preserved, the penultimate upper premolar (what we call P^4) is distinctly higher and piercing in *Kennalestes*, and possibly *Prokennalestes*, compared to the condition in *Gypsonictops* and "zhelestids." No clear phylogenetic inferences can be drawn from these differences, although one could reasonably argue that the reduction in size of P^3 and P_3 is derived, unless, of course, this is the retention of a normally smaller, deciduous tooth.

The relatively small size of the tooth at position three in most of the Late Cretaceous eutherians may indicate that it is a tooth undergoing evolutionary reduction and loss. In a study assessing dental homologies in both marsupials and placentals, Luckett (1993) noted that loss of a tooth at this position would be quite unusual given what we know concerning most extant and fossil placentals. He further noted that in an analysis under preparation he sug-
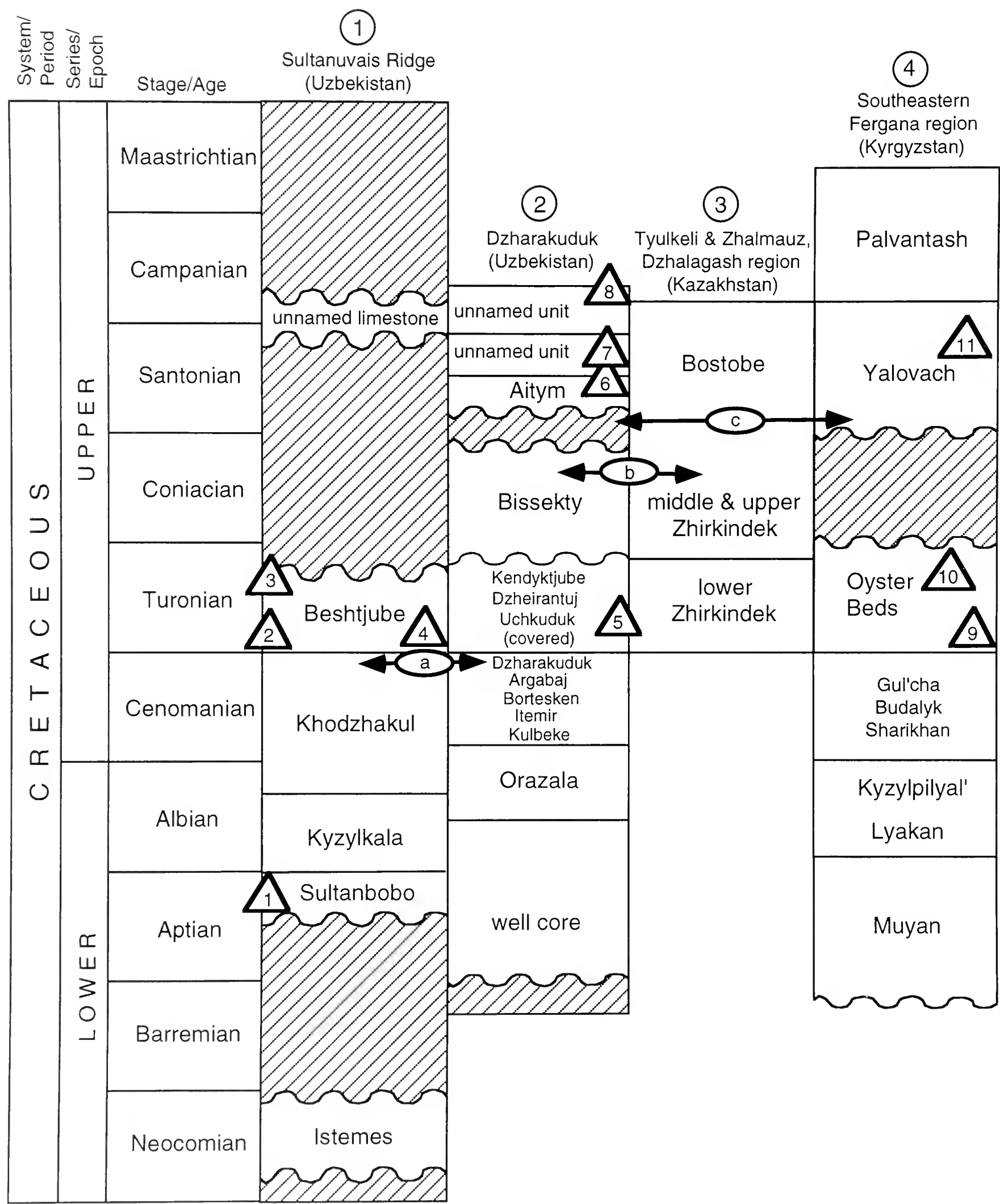
Fig. 5.—Cretaceous chronostratigraphic age estimates and correlations in western Asia. The four geological columns correspond to numbered localities shown in Figure 2. Numbered triangles are biostratigraphic age estimates as follows: 1, ammonites of *Acanthohoplites nolani* Zone, uppermost Aptian (Schultz, 1972); 2, ammonites of *Mammites nodosoides* Zone, lower Turonian (Schultz, 1972); 3, ammonites, upper Turonian (Schultz, 1972); 4, foraminiferans, lower Turonian (various sources); 5, foraminiferans, lower Turonian (Pyatkov et al., 1967), the ammonite *Proplacenticeras kharesmense* and the pelecypod *Inoceramus labiatus* 80 km east of Dzharakuduk

gests that this small tooth at position three may be a retained, reduced, deciduous P2. Supporting Luckett's argument that it is a retained deciduous premolar (whether dP2 or dP3) is the observation that only some individuals of *Gypsonictops hypoconus* and *Kennalestes gobiensis*, and, in one case, only one side of the dentary of *Kennalestes gobiensis*, possess this third position tooth. The small size and variable occurrence of this third premolariform tooth argues that evolutionary reduction was occurring, but does not clarify whether the tooth was deciduous or permanent. Its occurrence among as many as nine Late Cretaceous and two Early Cretaceous eutherian species does suggest, however, that possession of five such teeth is a primitive retention from an earlier stage in eutherian evolution.

The "zhelestid" material consists of isolated lower and upper teeth, some fragmentary maxillae or dentaries with teeth, and some edentulous maxillae and dentaries. As upper and lower teeth and jaws have not been found in occlusion and because of the fragmentary nature of the material, we cannot confidently match taxa based on upper and lower teeth, with one exception. We argue that the uppers of *Zhelestes bezelgen* can be associated with the lowers of *Aspanlestes aptap*, the latter name having priority. We also compare (Fig. 10) the uppers of *Zhelestes temirkazyk* with the lowers of a specimen referred to *Sorlestes budan*. These taxa may also be conspecific, but because of several similarly sized species known by uppers alone, we cannot confidently synonymize these two species.

Aspanlestes Nessov, 1985*a*

Type and Only Known Species.—*Aspanlestes aptap* Nessov, 1985*a*.

Distribution.—Late Cretaceous (late Turonian and Coniacian), western Uzbekistan.

Revised Diagnosis.—Same as for type and only species.

Aspanlestes aptap Nessov, 1985*a*
(Fig. 7, 8, 20, 21, 22F)

cf. *Cimolestes* (in part); Nessov, 1984*b*:63, unnumbered fig.
Aspanlestes aptap Nessov, 1985*a*:14, pl. 2, fig. 11; ?non-plate 2, fig. 10. Nessov et al., 1994:62, pl. 4, fig. 1; Archibald, 1996*b*: 1151, fig. 2E, F; 3C.
Aspanlestes cf. *aptap* Nessov, 1985*a*:pl. 2, fig. 7.
?*Zhelestes bezelgen* Nessov, 1987:207, pl. 1, fig. 1.
"Zhelestinae (Kennalestidae)" Nessov, 1987:pl. 1, fig. 3.
?non-?*Aspanlestes* sp. Nessov, 1987:pl. 6, fig. 6; Nessov, 1995: pl. 2, fig. 22.
Zhelestes bezelgen Nessov, 1987. Nessov and Kielan-Jaworowska, 1991:fig. 1; Nessov et al., 1994:63, pl. 5, fig. 1.
?*Zhelestes* sp., cf. *Z. bezelgen* Nessov, 1987. Nessov, 1993:125, pl. 2, fig. 3; pl. 5, fig. 5.

Holotype.—CCMGE 4/12176, right dentary with alveoli for P_3, crowns of P_{4-5}, M_{1-2}.

Type Locality.—Locality CDZH-17a, lower part of Bissekty Formation, Upper Cretaceous (upper Turonian), Dzharakuduk, western Uzbekistan.

Referred Specimens.—Lower dentition: CCMGE 6/12176, fragment of left dentary with talonid of M_2 and M_3; CCMGE 69/12455, left dentary with worn M_{2-3}; CCMGE 7/12953, chemically weathered right M_1; CCMGE 8/12953, left M_2; with some reservation, CCMGE 9/12953, left dentary fragment with one or more incisor alveoli, erupting canine, P_1 alveolus(i), P_2, anterior alveolus for P_3. Upper dentition: CCMGE 1/12455, left maxilla with three-rooted P^5, M^{1-2} (type of *Zhelestes bezelgen*); CCMGE 19/12953, right P^5 missing parastylar lobe; CCMGE 3/12455, left M^1; CCMGE 68/12455, left maxilla with alveoli for three-rooted P^5, alveoli for M^1, M^2, alveoli for M^3; IZANUz P No 2155-M-2, left M^2.

Localities.—All referred specimens except CCMGE 9/12953, 68/12455, and 7/12953 are from locality CBI-14, middle part of Bissekty Formation, Upper Cretaceous (Coniacian), Dzharakuduk, western Uzbekistan. CCMGE 9/12953 is from locality CDZH-17a, lower part Bissekty Formation (upper

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(Vereshchagin, 1979); 6, the shark *Hispidaspis* sp., larger specimens suggest Santonian or Campanian (Nessov, personal observation); 7, the ammonite *Placenticeras kysylkumense*, Santonian (A. A. Atabekijan, personal communication, 1994); 8, oysters and gastropods suggestive of middle to upper Campanian transgression (Nessov, personal observation); 9, marine pelecypods, lower Turonian (Verzilin, 1967); 10, ammonites, upper Turonian (Krymholts, 1977:table 12); 11, brackish-water pelecypods, same as Chinese Santonian species in northern Fergana (G. G. Martinson, personal communication). Numbered ellipsoids are correlations as follows: a, turtles *Kizylkumemys schultzi* and *Fergenemys* sp., cf. *F. itemirensis* in both the upper Khodzhakul Formation and Dzharakuduk Beds (Nessov, 1984*a*); b, similar or same hadrosaurids, crocodiles, and turtles in both the Bissekty and Zhirkindek formations (Nessov, personal observation); c, aridization at or near the Coniacian/Santonian boundary, with shift from grey to red beds and shift from relatively larger to smaller angiosperm leaves (Shilin, 1986), gars become locally extinct and are replaced by other "ganoid" fishes, taxonomic turnover in species of rays, crocodilians, and hadrosaurids (Nessov, personal observation).
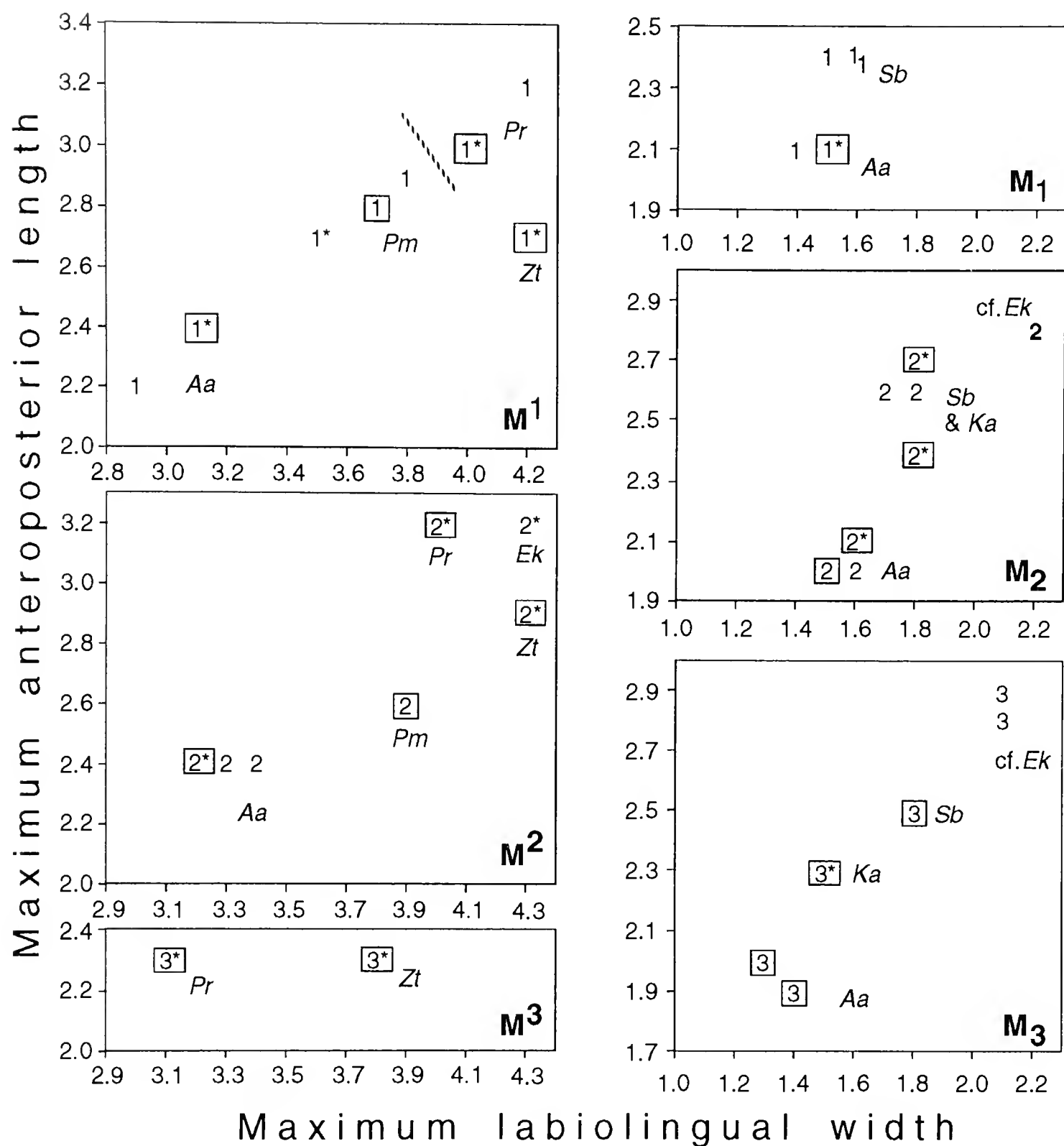
Fig. 6.—Graphs comparing maximum anteroposterior length (Y axis) versus maximum labiolingual width (X axis) for M¹, M², and M³ (left), and maximum length (Y axis) versus maximum width (X axis) for M₁, M₂, and M₃ (right). Measurements are those given in Tables 1 and 2. Numbers refer to tooth position. Numbers enclosed by squares are from dentary or maxilla, others are isolated teeth. Tooth positions for holotype specimens are identified by an asterisk. Dashed line in upper left graph given only to provide visual separation of species; it does not have statistical significance. Abbreviations are as follows: *Aa, Aspanlestes aptap* (including *Zhelestes bezelgen*); cf. *Ek*, cf. *Eoungulatum kudukensis*; *Ek, Eoungulatum kudukensis*; *Ka, Kumsuperus avus*; *Pm, Parazhelestes minor*; *Pr, Parazhelestes robustus*; *Sb, Sorlestes budan*; *Zt, Zhelestes temirkazyk*.

Turonian); CCMGE 68/12455 is from locality CBI-4, middle part, Bissekty Formation (Coniacian), and CCMGE 7/12953 is from locality CBI-5a, upper part of Bissekty Formation, (Coniacian); Upper Cretaceous, Dzharakuduk, western Uzbekistan.

Revised Diagnosis.—Compared with other "zhelestids": upper molar crowns slightly constricted through conular region, but similar to *Parazhelestes minor*; ectoflexus moderately deep; protocone with

slight anteroposterior expansion; protocone with little or no labial shift of apex; smallest in size. Of these five characters only the last might be an autapomorphy. The first four are shared with some or all other Late Cretaceous non-"zhelestids." Upper dentition averages 83% (ranging from 76–92% for three measurements each on P⁵, M¹, and M²) of size of next larger "zhelestid," *Parazhelestes minor*. As in lower dentition of other "zhelestids": trigonid

Table 1.—*Measurements (in mm) of Uzbek ungulatomorph upper dentitions. Italicized numbers are estimates. Daggers (†) indicate type specimens. Abbreviations are as follows: L, length; W, width; AW, anterior width; PW, posterior width.*

Specimen no.	P2		P4		P5			M1				M2				M3		
	L	W	L	W	L	AW	PW	L	AW	PW	L/PW	L	AW	PW	L/PW	L	AW	PW
Zhelestes temirkazyk																		
†10/12176	1.5	0.9	2.5	1.6	2.5	3.0	3.6	2.7	3.7	4.2	0.64	2.9	3.9	4.3	0.67	2.3	3.8	3.2
Aspanlestes aptap																		
3/12455	—	—	—	—	—	—	—	2.2	2.6	2.9	0.76	—	—	—	—	—	—	—
19/12953	—	—	—	—	—	—	2.6	—	—	—	—	—	—	—	—	—	—	—
†1/12455	—	—	—	—	2.0	2.2	2.7	2.4	2.6	3.1	0.77	2.4	2.9	3.2	0.75	—	—	—
68/12455	—	—	—	—	—	—	—	—	—	—	—	2.4	3.1	3.3	0.73	—	—	—
2155-M-2	—	—	—	—	—	—	—	—	—	—	—	2.4	3.2	3.4	0.71	—	—	—
Averages	—	—	—	—	—	—	2.7	2.3	2.6	3.0	—	2.4	3.1	3.3	—	—	—	—
Parazhelestes robustus																		
†70/12455	—	—	2.2	1.5	2.6	3.1	3.7	3.0	3.7	4.0	0.75	3.2	3.8	4.0	0.80	2.3	3.1	2.6
20/12953	—	—	—	—	—	—	—	3.2	3.8	4.2	0.76	—	—	—	—	—	—	—
10/12953	—	—	—	—	—	—	—	—	—	—	—	—	—	3.9	—	—	—	—
Averages	—	—	—	—	—	—	—	3.1	3.8	4.1	—	—	—	4.0	—	—	—	—
Parazhelestes minor																		
21/12953	—	—	—	—	—	—	3.2	—	—	—	—	—	—	—	—	—	—	—
22/12953	—	—	—	—	—	—	—	2.9	3.5	3.8	0.76	—	—	—	—	—	—	—
†11/12953	—	—	—	—	—	—	—	2.7	3.1	3.5	0.77	—	—	—	—	—	—	—
11/12176	—	—	—	—	2.4	2.9	3.3	2.8	3.3	3.7	0.76	2.6	3.7	3.9	0.67	—	—	—
12/12953	—	—	—	—	—	—	—	—	—	—	—	—	—	3.6	—	—	—	—
Averages	—	—	—	—	—	—	3.3	2.8	3.3	3.7	—	—	—	3.8	—	—	—	—
Eoungulatum kudukensis																		
†2/12455	—	—	—	—	—	—	—	—	—	—	—	3.2	4.0	4.3	0.74	—	—	—
cf. *Eoungulatum kudukensis*																		
35/12176	—	—	—	—	2.5	3.2	3.2	—	—	—	—	—	—	—	—	—	—	—

low relative to talonid, slight appression of paraconid and metaconid, pre- and postcingulids present, labial and lingual cingulids absent, entoconid and hypoconulid with some twinning, unlike in cf. *Eoungulatum kudukensis* and *Sorlestes budan* M_3 hypoconulid not posteriorly shifted and no suggestion of apical closure of cusps. Lower dentition averages 78% (ranging from 69–100% for two measurements each on P_4 and P_5, and for five measurements each on M_1 and M_2) of size of next larger "zhelestid," *Sorlestes budan*, and 72% (ranging from 67–87% for five measurements each on M_2 and M_3) of size of largest "zhelestid," cf. *Eoungulatum kudukensis*.

Description.—The maxilla of *Aspanlestes aptap* (CCMGE 1/12455; type of *Zhelestes bezelgen*) preserves two labial roots for the penultimate two-rooted premolar. As discussed under *Zhelestes temirkazyk*, this and the ultimate premolar are interpreted as P^4 and P^5, respectively. The P^5 in CCMGE 1/12455 (Fig. 7A), is a submolariform, three-rooted tooth. The well-developed protocone reaches as far lingually as the lingual margin of M^{1-2}. The stylar shelf is narrow and almost nonexistent labial to the paracone. The only stylar cusp is a well-developed parastyle formed as a distinct parastylar lobe. The metastyle lobe is also well de-

veloped, but lacks cusps. A prominent, slightly anteroposteriorly elongate paracone lacks a preparacrista, but has a distinct postparacrista that extends posterolabially onto the metastyle lobe. The postparacrista has a swelling in the region where a metacone would be expected. Distinct pre- and postparaconular cristae, and a subdued preprotocrista join, forming an indistinct paraconule. There is no metaconule or associated pre- and postmetaconule cristae. Very narrow but distinct pre- and postcingula are present. CCMGE 19/12953, a right P^5 missing the parastylar lobe, is similar in size to the P^5 in the type of *Z. bezelgen*, CCMGE 1/12455, and is tentatively referred to *Aspanlestes aptap*. This P^5 is slightly longer anteroposteriorly across the protocone. Two subdued cristae run posterolabially from the protocone. One is probably the postprotocrista, but the homology of the other is unknown. Except for the preceding differences and a slightly shorter, thicker paracone, this P^5 resembles the P^5 in the type maxilla.

In CCMGE 1/12455, M^{1-2} are similar except in the stylar region and the fact that M^2 is slightly narrower anteroposteriorly relative to its labiolingual width. On both M^1 and M^2, the stylar shelf is moderately wide labial to the metacone, forming a distinct metastylar lobe. The shelf remains relatively wide between the paracone and metacone, but narrows considerably labially to the paracone, especially on M^1. On both molars, there is a distinct parastylar lobe with a stylocone (formed by the juncture of the edge of the stylar shelf and the preparacrista), parastyle, and preparastyle. There are no other stylar cusps. The preparastyle appears to be present on M^2, but is partly obscured by the me-
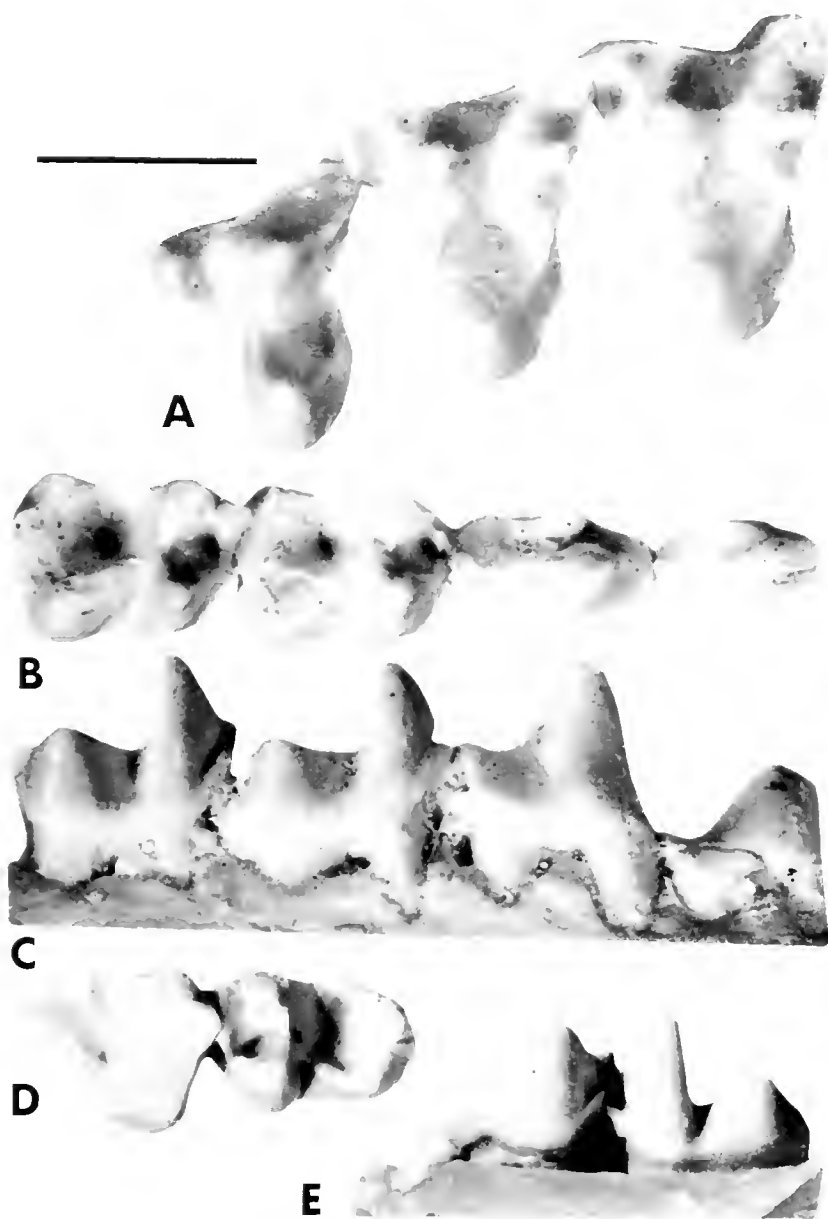
Fig. 7.—*Aspanlestes aptap* Nessov, 1985*a*. A. CCMGE 1/12455 (holotype of *Zhelestes bezelgen*), cast of left maxilla preserving P⁵–M² in occlusal view. B, C. CCMGE 4/12176, cast of holotype right dentary preserving P₄–M₂ in occlusal (B) and buccal (C) views. D, E. CCMGE 6/12176, cast of left dentary preseving talonid of M₂ and M₃ in occlusal (D) and buccal (E) views. Scale = 2 mm.

tastylar lobe of M^1. Also, CCMGE 68/12455, another M^2, has a preparastyle. The parastylar lobe is more labially expanded on M^2. As a result, there is a shallow but distinct ectoflexus on M^2, which is essentially absent on M^1. The following description refers to both M^1 and M^2. There are distinct pre- and postparacristae and distinct pre- and postmetacristae. The postmetacrista merges with the metastylar lobe. The paracone and metacone are similar in height, and both are moderately low. The paracone is only slightly larger in girth than the metacone. The well-developed paraconule and metaconule are situated relatively closer to the paracone and metacone than to the protocone. The conules have distinct pre- and postparaconule cristae and pre- and postmetaconule cristae forming prominent conular wings. The preparaconule and postmetaconule cristae continue labially, merging with the tooth below (dorsal to), respectively, the anterior margin of the paracone and posterior margin of the metacone. The apex of the protocone is as tall as the paracone and metacone. This cusp is lingually positioned, with some anteroposterior expansion. There are well-developed pre- and postcingula that begin lingually below the protocone, merging with the tooth below and just labial to the conules. One M^1 (CCMGE 3/12455) and two

M^2s (CCMGE 68/12455 and IZANUz P No 2155-M-2) are also tentatively referred to *Aspanlestes aptap*. They do not differ in any significant way from the above description of CCMGE 1/12455, except that one M^2, IZANUz P No 2155-M-2, is anteroposteriorly wider than is the case in CCMGE 1/12455. Although M^3 is unknown, the alveoli of M^3 in CCMGE 68/12455 (Nessov, 1993:pl. 2, fig. 3) show that this tooth was not reduced as the lingual margin of M^1 through M^3 are extended lingually to the same degree.

The following description of the lower dentition, except where noted, is based on the type, CCMGE 4/12176, a right dentary with alveoli for P_3, P_{4-5}, M_{1-2}; and CCMGE 6/12176, a fragment of the left dentary with a talonid of M_2 and M_3 (Fig. 7D, E). On P_{3-4}, the protoconid is the dominant cusp. On both, a cristid runs posteriorly from the apex of the protoconid to the posterior margin of the tooth, which divides the trenchant heel into a slightly larger lingual part and a smaller labial part. There are no distinct talonid cusps on either P_4 or P_5. On P_5, the lingual part of the talonid forms an incipient basin. A distinct, anteroposteriorly elongate metaconid and a narrow precingulid are found on P_5. Neither is present on the P_4. The dentary fragment CCMGE 9/12953, which we refer to *Aspanlestes aptap* with some reservation, preserves a P_2. It is similar to the P_4 just described, except that it is smaller, the cristid on the posterior side of the protoconid is faint, and the tooth is canted anteriorly. The molars do not differ greatly in length, with even the smallest molar, M_3 (preserved in CCMGE 6/12176; see Fig. 7D, E), only 0.2 mm shorter than the longest molars (see Table 2). This M_3, however, is considerably narrower than the talonid of M_2 preserved in the same dentary fragment (Fig. 7D). This suggests some labiolingual narrowing, but not anteroposterior shortening of M_3. All three molars are similar in having a distinct precingulid, narrower postcingulid, and no labial or lingual cingulids. On M_{1-2}, but less so on M_3, the hypoconulid is slightly closer to the entoconid (twinning) than to the hypoconid. On M_{1-2} the trigonid and talonid are of similar width, while on M_3 the talonid is narrower than the trigonid. On M_1 the trigonid and talonid are of similar length, but on M_{2-3} the trigonid is usually shorter. These length differences are the result of the differing placement of the paraconid on these molars. On M_1 the paraconid, which is rather crest-like, is near the anteroposterior midline, while on M_{2-3} it is distinctly more lingual. On M_1 the paraconid is less appressed to the metaconid than on M_{2-3}.

Discussion.—Aspanlestes aptap has the smallest lower teeth of any Asian "zhelestid." It closely corresponds in size to the upper molars of *Zhelestes bezelgen*. As shown in Figure 8, when the uppers and lowers of these taxa are superposed, the match is relatively good. We have little doubt that these two species belong to the same genus, *Aspanlestes*. At the species level, however, there are some apparent differences, all of which seem to relate to the size of the talonid in *Aspanlestes aptap*. As seen in Figure 8, the anteroposterior dimension of the protocone of M^1 and M^2 in the type of *Zhelestes bezelgen* appears to be slightly too large for the talonid basin of M_1 and M_2, respectively, in the type of *Aspanlestes aptap*. Further, almost 27 m of stratigraphic section separate the types of these two taxa.
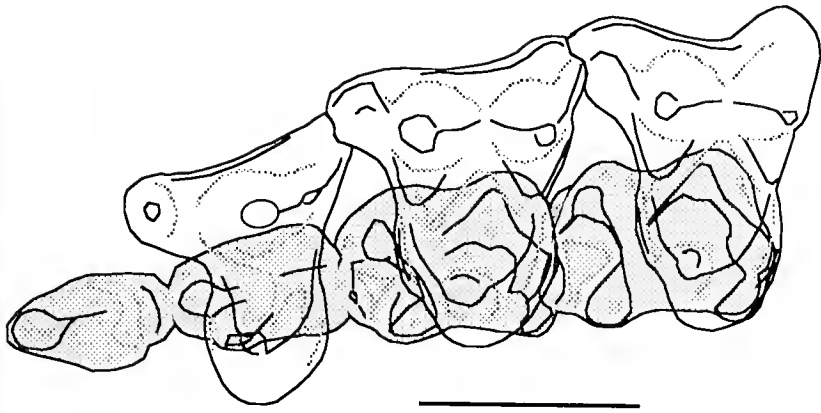
Fig. 8.—Superimposed occlusal outlines of the maxillary dentition of the holotype of *Zhelestes bezelgen* and the mandibular dentition (reversed) of the holotype of *Aspanlestes aptap*. The very close similarity in size and correspondence in occlusal morphology indicate that these specimens probably belong to the same species, *Aspanlestes aptap*. Scale = 2 mm.

Stratigraphic position is not an intrinsic character that is inherited and passed on, and thus should not be coded in a phylogenetic analysis; it may be, however, a cue that the above morphological differences are more than individual variation. Lacking more specimens to estimate whether this is specific or individual variation, we err on the side of the latter and tentatively treat *Zhelestes bezelgen* Nessov, 1987 as a junior synonym of *Aspanlestes aptap* Nessov, 1985a.

Based on the phylogenetic analysis presented later, *Aspanlestes aptap* retains more primitive character states relative to other "zhelestids." It is possible that this is an allometric phenomenon, which may or may not have a phylogenetic basis. Arguing against this is the fact that, of the two next larger Asian "zhelestids," one (*Zhelestes temirkazyk*) retains the next higher number of primitive retentions, while the other (*Parazhelestes minor*), does not. Thus, it is unclear whether size and retentions of primitive character states are in any way related.

Zhelestes Nessov, 1985a

Type and Only Known Species.—*Zhelestes temirkazyk* Nessov, 1985a.

Distribution.—Late Cretaceous (late Turonian and Coniacian), western Uzbekistan.

Revised Diagnosis.—Same as for type and only species.

Zhelestes temirkazyk Nessov, 1985a
(Fig. 9, 10, 20)

Zhelestes temirkazyk Nessov, 1985a:16, pl. 3, fig. 14. Nessov et al., 1994:63, pl. 5, fig. 1; Archibald, 1996b:1152, fig. 4A.
non-*Zhelestes* cf. *temirkazyk* Nessov, 1985a:16, pl. 3, fig. 5.

Holotype and Only Known Specimen.—CCMGE

10/12176, left maxilla with part of alveolus for large, single-rooted C^1, alveolus for small, single-rooted P^1, two-rooted P^2, bilobed root for small P^3, two-rooted P^4, three-rooted P^5, M^{1-3} (molars very worn).

Type and Only Known Locality.—Locality CBI-17, upper part of Bissekty Formation, Upper Cretaceous (Coniacian), Dzharakuduk, western Uzbekistan.

Revised Diagnosis.—Of the following character states, only the relative narrowness of M^1 and M^2 are arguably autapomorphic for *Zhelestes temirkazyk*. Upper molar crowns not constricted through conular region as is also the case in other Asian ungulatomorphs except *Aspanlestes aptap* and *Parazhelestes minor*; at least shallow ectoflexus as found in all "zhelestids" except *Eoungulatum kudukensis*; protocone with slight anteroposterior expansion as is also the case in *Aspanlestes aptap*; protocone with little or no labial shift of apex as is also the case in *Aspanlestes aptap*, although this is conjectural because of extreme wear; closest in size to *Parazhelestes robustus* and *P. minor*. Compared with other "zhelestids": upper molar crowns anteroposteriorly shorter (narrower) relative to labiolingual width, with a ratio of 0.64 for M^1 compared to an average of 0.77 for all other known Asian "zhelestid" M^1s (seven specimens) and a ratio of 0.67 for M^2 compared to an average of 0.73 for all other known Asian "zhelestid" M^2s (six specimens). The narrowness of M^2 is only matched by that of M^2 in *Parazhelestes minor*.

Description.—The occlusal surfaces are obliterated by dental attrition on most occlusal surfaces in the single specimen known for *Zhelestes temirkazyk*, so that little can be described of the crown morphology. Much of the left maxillary region is preserved, however, providing considerable information (Fig. 9, 10).

The posterior margin of a large canine alveolus and an alveolus for a single-rooted P^1 are preserved, as are a little-worn, two-rooted P^2, single-rooted fragment of a smaller P^3, somewhat worn P^{4-5}, and very heavily worn M^{1-3}. A large infraorbital foramen lies dorsal to the posterior root of P^4. The two-rooted P^2 has a single dominant cusp with a small anterior cingular cuspule and a posterior margin that is slightly expanded but which bears no cusps. Unlike P^2, which is implanted vertically, P^4 is canted slightly posteriorly because the anterior root slants posteriorly before joining the crown. P^4 is probably only two-rooted, but the posterior margin is linguolabially expanded into an incipient protocone. The crown is dominated by a single cusp, but there are also anterior cingular and posterior cingular cuspules. The P^3 root shows this to be a smaller tooth than P^2 or P^4. P^5 is slightly less worn than the molars. It is a submolariform, three-rooted tooth. The well-developed protocone reaches as far lingually as the lingual margin of M^{1-2}. The stylar shelf is narrow, being almost nonexistent labial to the paracone. A parastyle appears to be the only stylar cusp on a distinct parastylar lobe. The metastylar lobe
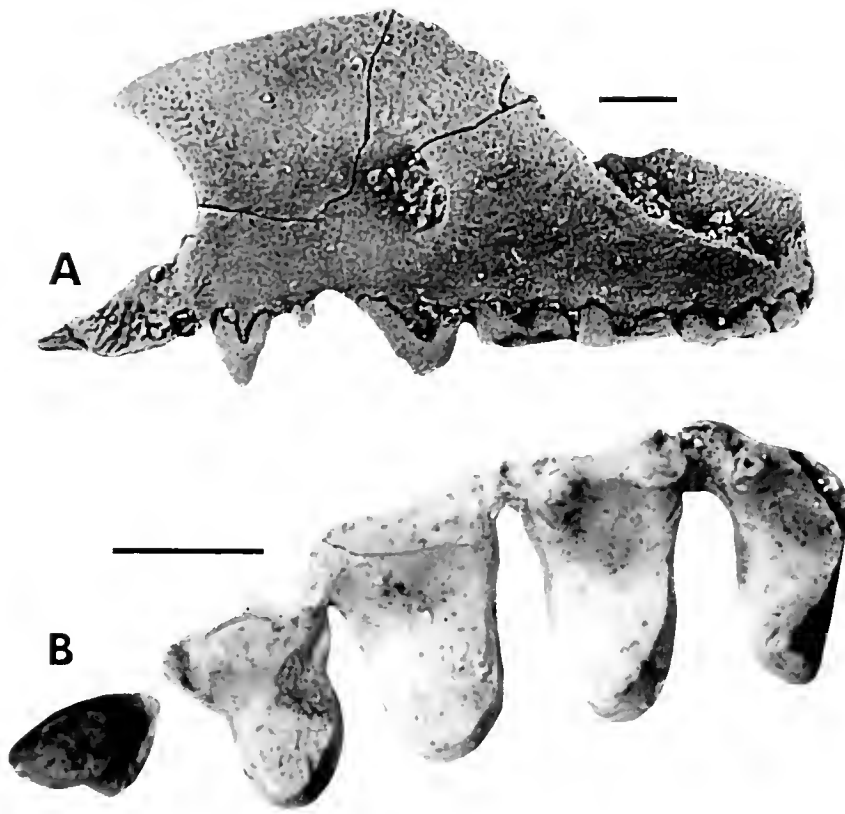
Fig. 9.—*Zhelestes temirkazyk* Nessov, 1985a, CCMGE 10/12176, holotype left maxilla preserving part of alveolus for large, single-rooted C^1; alveolus for small, single-rooted P^1; crown of P^2; roots of small P^3; crowns of P^4–M^3 in labial (A) and occlusal (B) views. Scales = 2 mm.

Fig. 10.—Left labial view of maxilla of *Zhelestes temirkazyk* shown in Figure 9 compared to dentary of *Sorlestes budan* shown in Figure 19D–F. Lower view is occlusal view of dentary showing alveoli. Reconstructed teeth are shown by dotted lines. Diagonal lines are broken areas. Stippling on dentary shows alveoli. Stippling on maxilla shows suture with jugal. Note the evidence for five premolars in maxilla, and relative size of premolars, $P^5 > P^4 > P^2 > P^3 > P^1$. Scale = 2 mm. See text for discussion.

is also well developed, but lacks cusps. The prominent but heavily worn paracone preserves a distinct postparacrista with an obvious swelling, suggesting that a metacone may have been present. There are very narrow and possibly worn pre- and postcingula.

The occlusal surfaces of M^{1-3} are nearly obliterated, so that nothing can be said about the disposition (or even presence or absence) of the conules and their related cristae. It does appear that the molars possessed pre- and postparacristae and pre- and postmetacristae. The stylar shelves are moderately narrow except for the parastylar region on M^{2-3} and the metastylar region on M^{1-2}. With both para- and metastylar lobes, M^2 has a distinct but shallow ectoflexus. There appear to be three cusps on the parastylar lobe on at least M^1: stylocone, parastyle, and preparastyle. There is a distinct cuspule on the metastylar lobe of M^2. Otherwise, the crowns are so worn that wear has reached to the level of the narrow, but distinct pre- and postcingula.

Discussion.—Even with considerable wear, enough morphology is preserved that there is little doubt that *Zhelestes temirkazyk* is a "zhelestid." In Figure 10 these affinities are reinforced by a comparison of the type of *Zhelestes temirkazyk* with a dentary referred here to *Sorlestes budan*. This comparison permits a suggested reconstruction for missing teeth in both species. Most notable is the assessment of five premolars in both the upper and lower jaws. Further, P^3 and P_3 appear to be smaller than adjacent P^2 and P_2, and P^4 and P_4. We refer an edentulous dentary (Fig. 19A) to "Zhelestidae" because it possesses this same size pattern and also because it is similar in size to the larger Asian "zhe-

lestids." As discussed previously under "Zhelestidae," we have no clear evidence as to whether the smaller, third tooth between the canine and molars is a permanent premolar or a retained deciduous tooth.

Parazhelestes Nessov, 1993

Type Species.—*Parazhelestes robustus* Nessov, 1993.

Included Species.—Type species and, tentatively, *Parazhelestes minor*, n. sp.

Distribution.—Late Cretaceous (Coniacian), western Uzbekistan.

Revised Diagnosis.—Upper molar crowns only slightly (*Parazhelestes minor*) or not constricted through conular region (*Parazhelestes robustus*) as is also the case in other Asian "zhelestids"; at least shallow ectoflexus as found in all "zhelestids" except *Eoungulatum kudukensis*; protocone intermediate among "zhelestids" in amount of anteroposterior expansion and amount of labial shift of apex; intermediate in size among "zhelestids"; M^3 markedly linguolabially narrowed compared to M^{1-2} in *P. robustus* (condition unknown in *Parazhelestes minor*).

Comments.—Without knowledge of the size of M^3 in *Parazhelestes minor*, it is difficult to be con-

fident regarding the referral of this species to *Parazhelestes*. *Parazhelestes robustus* and *P. minor* show a similar degree of labial shift of the protocone relative to that seen in *Aspanlestes aptap* and *Eoungulatum kudukensis*. Depending on whether *P. minor* ultimately proves to have M³ markedly linguolabially narrowed compared to M¹⁻², this character is either an autapomorphy of *Parazhelestes* or of *P. robustus*.

Parazhelestes robustus Nessov, 1993
(Fig. 11, 20, 21)

Parazhelestes robustus Nessov, 1993:124, pl. 2, fig. 1; note that this figure was incorrectly published at 87% of the size indicated in the figure caption, as were all others in Nessov, 1993.

Holotype.—CCMGE 70/12455, left maxilla with two-rooted P⁴, three-rooted P⁵, worn M¹–M³.

Type Locality.—Locality CBI-14, middle part of Bissekty Formation, Upper Cretaceous (Coniacian), Dzharakuduk, western Uzbekistan.

Referred Specimens.—CCMGE 20/12953, left M¹, and CCMGE 10/12953, worn and damaged right M².

Localities.—All referred specimens are from the type locality.

Revised Diagnosis.—Compared to *Parazhelestes minor*: size averages about 10% larger (ranging from 3–19% for three measurements each on the P⁵, M¹, and M²); molar crowns not constricted through conular region; M² less linguolabially extended.

Description.—The type maxilla, CCMGE 70/12455 (Fig. 11A), preserves a two-rooted penultimate premolar and a three-rooted ultimate premolar, which, as discussed under *Zhelestes temirkazyk*, are interpreted as P⁴⁻⁵. P⁴ is dominated by a single cusp, but there are also anterior cingular and posterior cingular cuspules. The posterior margin is linguolabially expanded into an incipient protocone. P⁵ is a submolariform, three-rooted tooth. The well-developed protocone reaches as far lingually as the lingual margin of M¹⁻² and is anteroposteriorly wide compared with the same region in *Aspanlestes aptap* and *Zhelestes temirkazyk*. The stylar shelf is narrow, being almost nonexistent labial to the paracone. A parastyle appears to be the only stylar cusp on a distinct parastylar lobe. The metastylar lobe is also well developed and bears a single cuspule. Although somewhat worn and slightly damaged, there is a distinct metacone swelling and a metacone may have been present. The centrocrista (postparacrista + premetacrista) and postmetacrista are well developed, but there is no preparacrista. There appears to have been a small postparaconular crista but no premetaconular crista. There is only a hint of widening in the area of the pre- and postcingula.

In CCMGE 70/12455 M¹⁻² (Fig. 11A) are similar except for the stylar region and the fact that M¹ is slightly wider anteroposteriorly, with more distinct pre- and postcingula. On both M¹ and M² the stylar shelf is generally narrower than in either *Aspanlestes aptap* or *Zhelestes temirkazyk* (Fig. 20). The shelf remains recognizable between the paracone and metacone. It nar-

rows considerably labial to the paracone on both M¹⁻², but this narrowing is slightly less pronounced labial to the metacone on both molars. The remainder of the molar description is based mostly on a very well-preserved left M¹, CCMGE 20/12953 (Fig. 11B–F). The less worn and damaged parts of the type maxilla, CCMGE 70/12455, and a left M², CCMGE 10/12953, agree with this description. On CCMGE 20/12953 there is a distinct parastylar lobe on which there are three small cuspules: stylocone, parastyle, and preparastyle. There is also a small, distinct metastyle labial to the metacone. The postparacrista, and pre- and postmetacristae are distinct, but the preparacrista is not expressed on most of the height of paracone, but is present near its base. This crista, although worn, seems slightly better developed on the M¹⁻² in the type maxilla. This may be the result of considerable dental attrition of the parastylar groove, which accentuated the unworn area of the preparacrista. The postmetacrista merges with the metastylar lobe. The paracone and metacone are similar in height, which is moderately low, and they are separate at their bases. The well-developed paraconule and metaconule are situated approximately midway between the paracone and metacone labially and the protocone lingually. The conules have distinct pre- and postparaconule cristae and pre- and postmetaconule cristae, forming prominent conular wings. The preparaconule crista continues anterolabially, forming a broad paracingulum with the parastylar lobe. The postmetacrista forms the metacingulum, which merges with the tooth below (dorsal to) the posterior margin of the metacone. The apex of the protocone is as tall as the paracone and metacone. This cusp lies approximately on the middle of the lingual half of the M¹, as it is in *Parazhelestes minor*, but is more labial than in *Aspanlestes aptap* and more lingual than in *Eoungulatum kudukensis* (Fig. 21). The degree of anteroposterior expansion of the protocone is also intermediate between conditions in the latter two taxa. There are well-developed pre- and postcingula beginning lingually below the protocone, merging with the tooth below and just labial to the conules. CCMGE 20/12953 shows a slight amount of constriction of the crown through the conular area (slightly exaggerated in Fig. 11B), which is not seen in the other two specimens. The surface of M³ in the type specimen is obscured by wear, but there is no doubt that this tooth is considerably narrower linguolabially than M¹⁻² (Fig. 11A). M³ in *P. robustus* is also narrower than that in *Zhelestes temirkazyk*; alveoli for this tooth in a maxilla of *Aspanlestes aptap* (see earlier description) suggest that *Zhelestes temirkazyk* and *Aspanlestes aptap* were similar for this character.

Parazhelestes minor, **new species**
(Fig. 12, 13, 20, 21)

Zhelestes cf. *temirkazyk* Nessov, 1985a:16, pl. 3, fig. 5.
"gen. indet." Nessov et al., 1994, pl. 7, fig. 8.
Parazhelestes n. sp. Archibald, 1996b:1151, fig. 2G, H.

Holotype.—CCMGE 11/12953, right M¹.

Type Locality.—Locality CBI-4, middle part of Bissekty Formation, Upper Cretaceous (Coniacian), Dzharakuduk, western Uzbekistan.

Referred Specimens.—CCMGE 11/12176, right maxilla with two roots of P⁴, three-rooted P⁵, M¹⁻², all showing some wear; CCMGE 21/12953, right P⁵ lacking the parastylar lobe; CCMGE 22/12953, left M¹; CCMGE 12/12953, right M².

Localities.—All referred specimens are from lo-
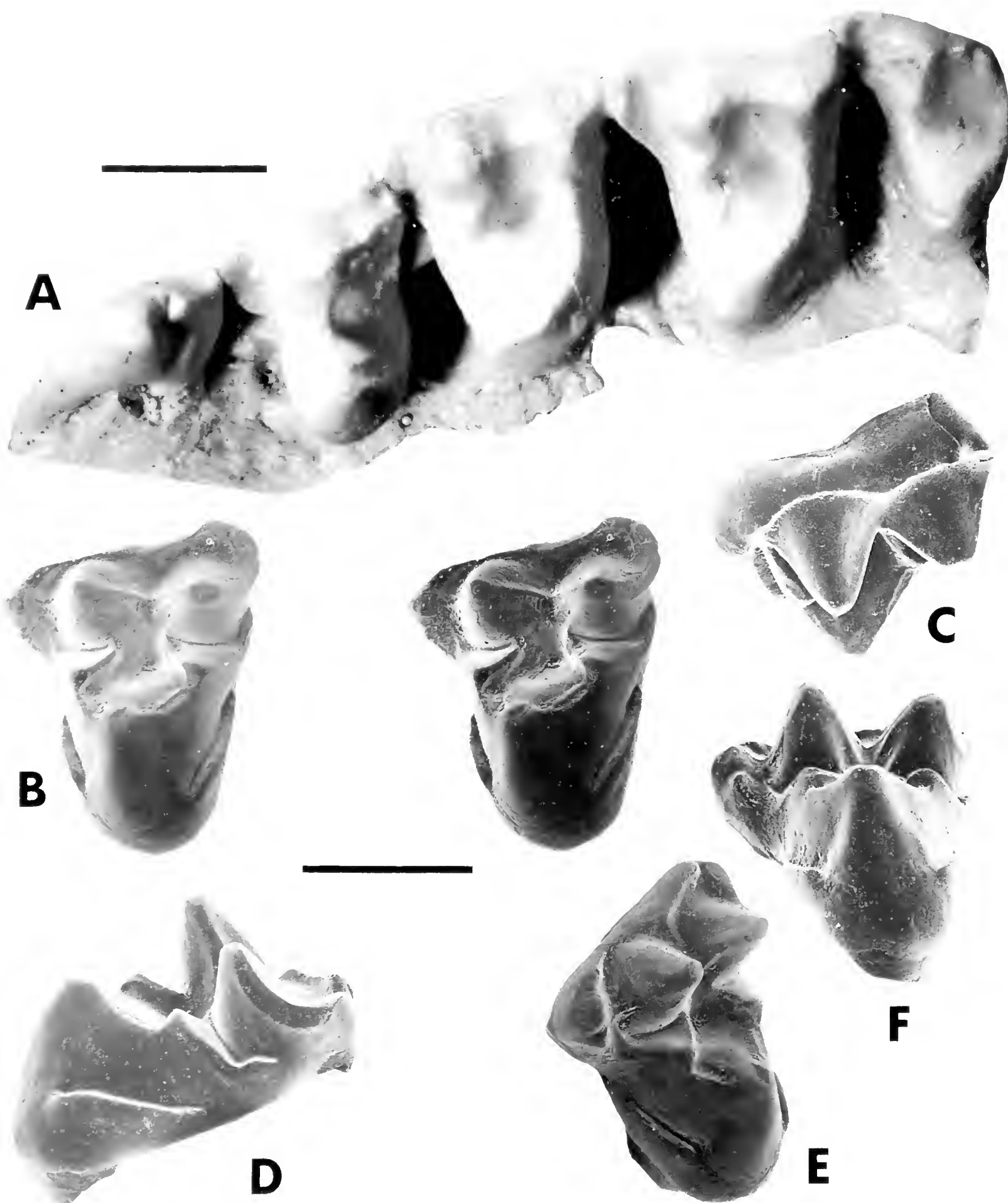
Fig. 11.—*Parazhelestes robustus* Nessov, 1993. A. CCMGE 70/12455, cast of holotype left maxilla preserving P^4–M^3 in occlusal view. B–F. CCMGE 20/12953, left M^1 in occlusal (B), buccal (C), posterior (D), anterior oblique (E), and lingual (F) views. Occlusal view in B is stereopair. Scales = 2 mm (upper scale corresponds to A, lower scale corresponds to B–F).

cality CBI-14, middle part of Bissekty Formation, Upper Cretaceous (Coniacian), Dzharakuduk, western Uzbekistan.

Etymology.—Latin *minor*, less. In reference to the smaller size of this species compared to *P. robustus*.

Diagnosis.—Compared to *Parazhelestes robustus*: size averages about 10% smaller (ranging from 3–19% for three measurements each on the P^5, M^1, and M^2); molar crowns slightly constricted through the conular region; M^2 more linguolabially extended.
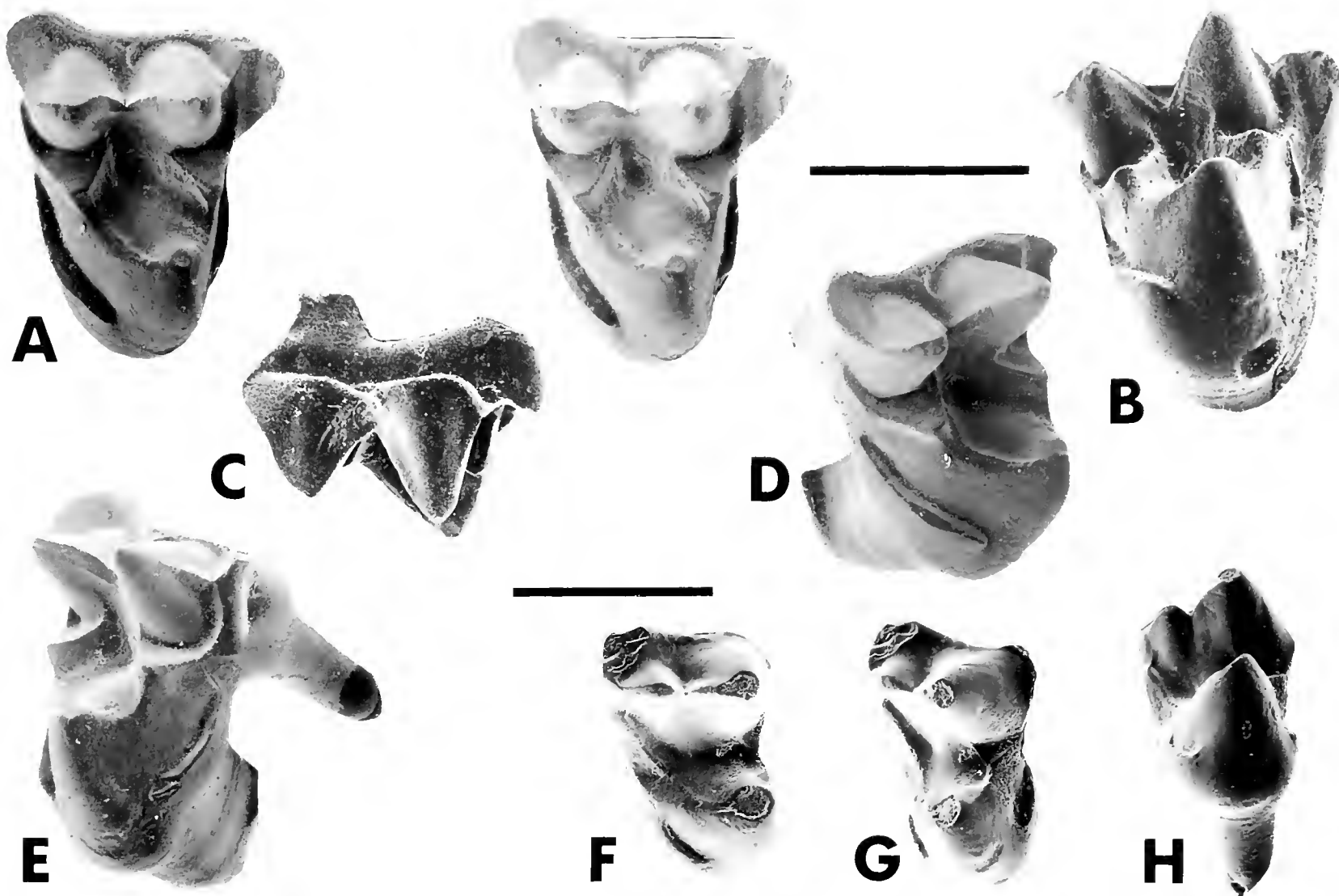
Fig. 12.—*Parazhelestes minor*, n. sp. A–E. CCMGE 11/12953, holotype right M¹ in occlusal (A), lingual oblique (B), buccal (C), posterior oblique (D), and anterior oblique (E) views. Occlusal view in A is stereopair. F–H. CCMGE 21/12953, right P⁵ lacking the parastylar lobe in occlusal (F), anterior oblique (G), and lingual oblique (H) views. Scales = 2 mm (upper scale corresponds to A–E, lower scale corresponds to F–H).

Description.—CCMGE 11/12176, a right maxilla, preserves two roots of P⁴ and a three-rooted P⁵, as well as M¹⁻², all showing some wear (Fig. 13). An isolated P⁵, CCMGE 21/12953, lacking the parastylar lobe, differs from the P⁵ in the maxilla in some possibly significant ways (Fig. 12F–H). Because of their close similarity in size, however, the P⁵s seem best referred to the same species for now. Both P⁵s are submolariform, three-rooted teeth. The well-developed protocone on P⁵ reaches as far lingually as the lingual margin of M¹⁻² in CCMGE 11/12176, and is only exceeded by *Parazhelestes robustus* in terms of its anteroposterior dimension. The stylar shelf is narrow, being almost nonexistent labial to the paracone. The parastylar lobe, which is distinct, is preserved only on the P⁵ on CCMGE 11/12176. It is sufficiently worn that no cuspules can be recognized, if indeed they were present. A small preparacrista is detectable at the base of the paracone. Both P⁵s preserve a well-developed metastylar lobe, neither of which have cuspules. The centrocrista and postmetacrista are well developed on both P⁵s. CCMGE 11/12176, however, has only a very slight swelling in the region of the metacone, while the isolated P⁵, CCMGE 21/12953, has a small but distinct metacone. Both P⁵s have distinct but weak pre- and postparaconular cristae, so that a small paraconule is defined. Both lack a premetaconule crista, but the isolated P⁵ has a postmetaconule crista. Narrow but distinct pre- and postcingula are present on the isolated P⁵. Only the postcingulum is similarly developed on the P⁵ in the maxilla, while there is only a hint of a precingulum.

The upper molars referred to *Parazhelestes minor* have a narrow stylar shelf compared with most other Late Cretaceous eutherians; this structure appears to be slightly wider than in *Parazhelestes robustus* but similar to that in *Aspanlestes aptap* and *Zhelestes temirkazyk* (Fig. 20). The shelf remains recognizable between the paracone and metacone. It narrows considerably labial to the paracone on both M¹ and M², but is slightly broader labial to the metacone on both molars. The type specimen, CCMGE 11/12953, is the best preserved, although it is the smallest of the three M¹s referred to *P. minor* (Fig. 12A–E). It compares favorably in most respects with the well-preserved M¹, CCMGE 20/12953, assigned to *Parazhelestes robustus* (Fig. 11B–F). The photographs suggest that the protocone is slightly more labial in *Parazhelestes robustus*. This is illusory because when posterior outlines of these M¹s are drawn to the same size, they almost completely overlap (top position, Fig. 21). The metastylar and parastylar lobes are both well developed on referred M¹s and M²s. There are no cuspules on the metastylar lobe. The ridge bordering the stylar shelf is interrupted on M² in the maxilla (CCMGE 11/12176), with the edges bordering this interruption being slightly swollen. On less worn M¹s and M²s, there are three cuspules on the parastylar lobe: stylocone, parastyle, and preparastyle. The postparacrista, and pre- and postmetacristae are distinct and present on all molars. The preparacrista is present on all the molars, but is usually more subdued. The postmetacrista merges with the metastylar lobe. The paracone and metacone are both moderately low and are separate at their bases. The

Fig. 13.—*Parazhelestes minor*, n. sp., CCMGE 11/12176, cast of right maxilla preserving roots for P⁴ and crowns of P⁵–M² in occlusal view. Scale = 1 mm.

well-developed paraconule and metaconule are situated approximately midway between paracone and metacone on the one hand and protocone on the other. The conules have distinct pre- and postparaconule cristae and pre- and postmetaconule cristae, forming prominent conular wings. The preparaconule crista continues anterolabially, forming a well-defined paracingulum with the parastylar lobe. The postmetacrista forms the metacingulum, which merges with the tooth below (dorsal to) the posterior margin of the metacone. The apex of the protocone is as tall as the paracone and metacone. This cusp is situated approximately on the middle of the lingual half of M¹, as it is in *Parazhelestes robustus*, but is more labial than in *Aspanlestes aptap* and more lingual than in *Eoungulatum kudukensis* (Fig. 21). The degree of anteroposterior expansion of the protocone is similar to that in *Parazhelestes robustus*. There are well-developed pre- and postcingula beginning lingually below the protocone, merging with the tooth below and just labial to the conules. The molars show a slightly greater degree of constriction of the crown through the conular area compared to *Parazhelestes robustus*.

Comments.—There is enough variation in size and morphology of the three M¹s placed in *Parazhelestes minor* to question whether only one species is represented. The problem, however, is that we do not have enough upper molars of any "zhelestid" to investigate meaningfully the issue of variation. The holotype M¹, CCMGE 11/12953, is the smallest of these M¹s. It is also the least worn (Fig. 12A–E). It is very similar to the somewhat worn M¹ in the maxilla, CCMGE 11/12176 (Fig. 13), except that the M¹ in the maxilla is slightly larger, has a less lingually extended postcingulum, has a slightly larger parastylar lobe, and has a protocone with a slightly more expanded lingual face. The most heavily worn M¹ referred to *P. minor*, CCMGE 22/12953, in addition to being larger than the holotype, has a relatively more lingually extended pro-

tocone and is relatively narrower across the conular region. This tooth may belong to *Zhelestes temirkazyk*, or it may be an M² of *P. minor* rather than an M¹. The latter possibility seems more likely.

Eoungulatum, **new genus**

Type and Only Known Species.—*Eoungulatum kudukensis*, n. gen. and sp.

Distribution.—Late Cretaceous (Coniacian), western Uzbekistan.

Etymology.—Greek *eos*, dawn, early; and Latin *ungula*, hoof. In reference to the very early age and resemblance to archaic ungulates.

Diagnosis.—Same as for type and only known species.

Eoungulatum kudukensis, **new species**
(Fig. 14A–E, 20, 21, 19I)

"Advanced form of Proteutheria, intermediate to Condylarthra" Nessov, 1987, pl. 1, fig. 2.
"Archaic ungulate mammals" Nessov and Kielan-Jaworowska, 1991, fig. 1, shown as left M².
"Condylarthra of the family Periptychidae" Nessov, 1993, pl. 1, fig. 3 (not pl. 6, as indicated in Nessov, 1993).
"gen. et sp. nov." Archibald, 1996b:1151, fig. 2D, 3D.

Holotype and Only Known Specimen.—CCMGE 2/12455, left M².

Type Locality.—Locality CBI-14, middle part of Bissekty Formation, Upper Cretaceous (Coniacian), Dzharakuduk, western Uzbekistan.

Etymology.—Kazak *kuduk*, well. In reference to the general Dzharakuduk region, which means "well near the escarpment" in Kazak, where the type and tentatively referred specimens were found.

Diagnosis.—Compared with other "zhelestids": upper molar crown without ectoflexus; protocone with greatest anteroposterior expansion; protocone with greatest labial shift of apex; largest in size. Upper dentition is comparable in length, but about 6% wider (only two measurements of M²) than the slightly smaller "zhelestid," *Parazhelestes robustus*. If the lower teeth described below are correctly referred to *E. kudukensis*, the lower dentition averages 8% (three measurements of M₂) greater in length and 20% (two measurements of M₂) greater in width than the slightly smaller *Sorlestes budan*.

Description.—The holotype, a left M² (CCMGE 2/12544) has three roots. The enamel shows chemical weathering that obscures some details of the crown. The occlusal outline of the crown is nearly rectangular, with the lingual part almost as long as the labial. The parastylar lobe is quite prominent, but the metastylar region is less so. The stylar shelf is narrow, with no distinct ectoflexus. There may have been three cuspules on the parastylar

lobe: preparastyle, parastyle, and stylocone. There are small bumps on the stylar shelf labial to both the paracone and metacone, but we cannot determine if these are real or a result of weathering. There may not have been a preparacrista, but a prominent postmetacrista extends from the metacone to the metastylar region. The paracone and metacone are conical and similar in size, with an indistinct (possibly because of wear) centrocrista. The apices of both the paracone and metacone are broken. As in all other upper molars of "zhelestids," the para- and metaconules have prominent wings with strong cristae forming especially strong shearing facets on their internal surfaces. The preparaconule crista forms a narrow, continuous paracingulum that merges labially with the parastylar lobe. The postmetaconule crista forms a narrow metacingulum that continues labially below (dorsal to) the metacone, where it terminates. The protocone is the largest cusp, with a broad, rounded lingual face and well-developed but subdued (possibly because of weathering) pre- and postprotocristae. Both the pre- and postcingula, but especially the precingulum, are weathered. The precingulum originates as a faint vertical crest below the paracingulum. It then turns horizontally and broadens slightly to form the precingulum. Just anterior to the protocone it narrows to form a faint triangular facet on the anterior face of the protocone. It broadens slightly again as it continues to form a lingual cingulum that merges with the postcingulum. There is a slight apical expansion of the postcingulum posterolingually below the protocone (in the position of a hypocone). The postcingulum then narrows slightly, and continues around the posterior margin of the molar. At a point between and below the metaconule and metacone, the postcingulum becomes very narrow, sharply turns vertically, and contacts the metacingulum.

cf. *Eoungulatum kudukensis*, new species
(Fig. 14F–Q, 20)

Four specimens probably belong to *Eoungulatum kudukensis* based on size and morphology, but given the fragmentary nature of the material, a more definite assignment is not currently possible. These specimens are: CCMGE 35/12176, right P^5; CCMGE 17/12953, right M_2; CCMGE 18/12953, left M_3; CCMGE 16/12953, left M_3. CCMGE 17/12953, CCMGE 18/12953, and CCMGE 16/12953 are from locality CBI-14, and CCMGE 35/12176 is from locality CBI-4b, middle part of Bissekty Formation, Upper Cretaceous (Coniacian), Dzharakuduk, western Uzbekistan.

The right P^5, CCMGE 35/12176 (Fig. 14P, Q, 20), could easily be mistaken for the ultimate upper premolar of a small periptychid, even though this family is unknown in the fossil record until some 20 million years later. There is no stylar shelf. The metastylar and parastylar lobes are small, as in the holotype M^2 of *Eoungulatum kudukensis*. The paracone and protocone are both robust, slightly swollen, and worn apically. There is a distinct metacone swelling. Probably because of cusp swelling, there are no cristae between or emanating from the paracone and metacone. There are traces of pre- and

postparaconule cristae and there may have been a paraconule. Para- and metacingula are present. Unlike on P^5s or upper molars of other "zhelestids," but as in archaic ungulates, the metacingulum is at the level of and continues onto the metastylar lobe. There are narrow pre- and postcingula.

The three lower molars that may belong to *Eoungulatum kudukensis*, one M_2 and two M_3s, seem to cluster together based on size (Fig. 6). In morphology, however, there is some indication that at least two taxa may be represented. The lower molar that seems most likely to belong to *E. kudukensis* is a left M_3, CCMGE 16/12953 (Fig. 14F–J). As in other "zhelestids," the trigonid is low relative to the talonid compared with other Late Cretaceous eutherians. The overall height of both the trigonid and talonid appear to be greater than in any other "zhelestid." The paraconid is almost, but not completely lingual, and is slightly appressed to the larger metaconid. As in other "zhelestids" there are small pre- and even smaller postcingulids, but no labial or lingual cingulids. Individual cusps do not appear to be swollen, but the whole crown is slightly swollen at its base, so that the apices of the cusps seem slightly more crowded. This is especially clear for the talonid basin and the talonid cusps. This closure of the cusps is seen to a much greater extent in some earlier Tertiary periptychids. There seems to be little or no twinning of hypoconulid and entoconid, probably because the hypoconulid is set slightly separate and more posterior. This more posterior placement of the hypoconulid on M_3 is seen to a greater extent in many, if not all, early Tertiary archaic ungulates.

The other M_3, CCMGE 18/12953, is only slightly larger than CCMGE 16/12953; the trigonid and talonid widths are comparable in the two, but the talonid is relatively longer in the former specimen (Table 2). The height of both the trigonid and the talonid are less than on CCMGE 16/12953. The base of the crown has little or no swelling and the apices of the cusps do not seem to show crowding, although there is some wear. The hypoconulid shows slight twinning with the entoconid, but as in CCMGE 16/12953, it is positioned more posteriorly than in M_2s. The trigonid and its cusps are comparable on the two M_3s. In CCMGE 18/12953 the pre- and postcingulids are not as small, and there is a small ectostylid. Based on overall size, the next possible candidate to which CCMGE 18/12953 might be referred is *Parazhelestes robustus*. In this species, however, M_3 is labiolingually reduced, yet there is no sign of such a reduction in CCMGE 18/12953. The next likely candidate based on size
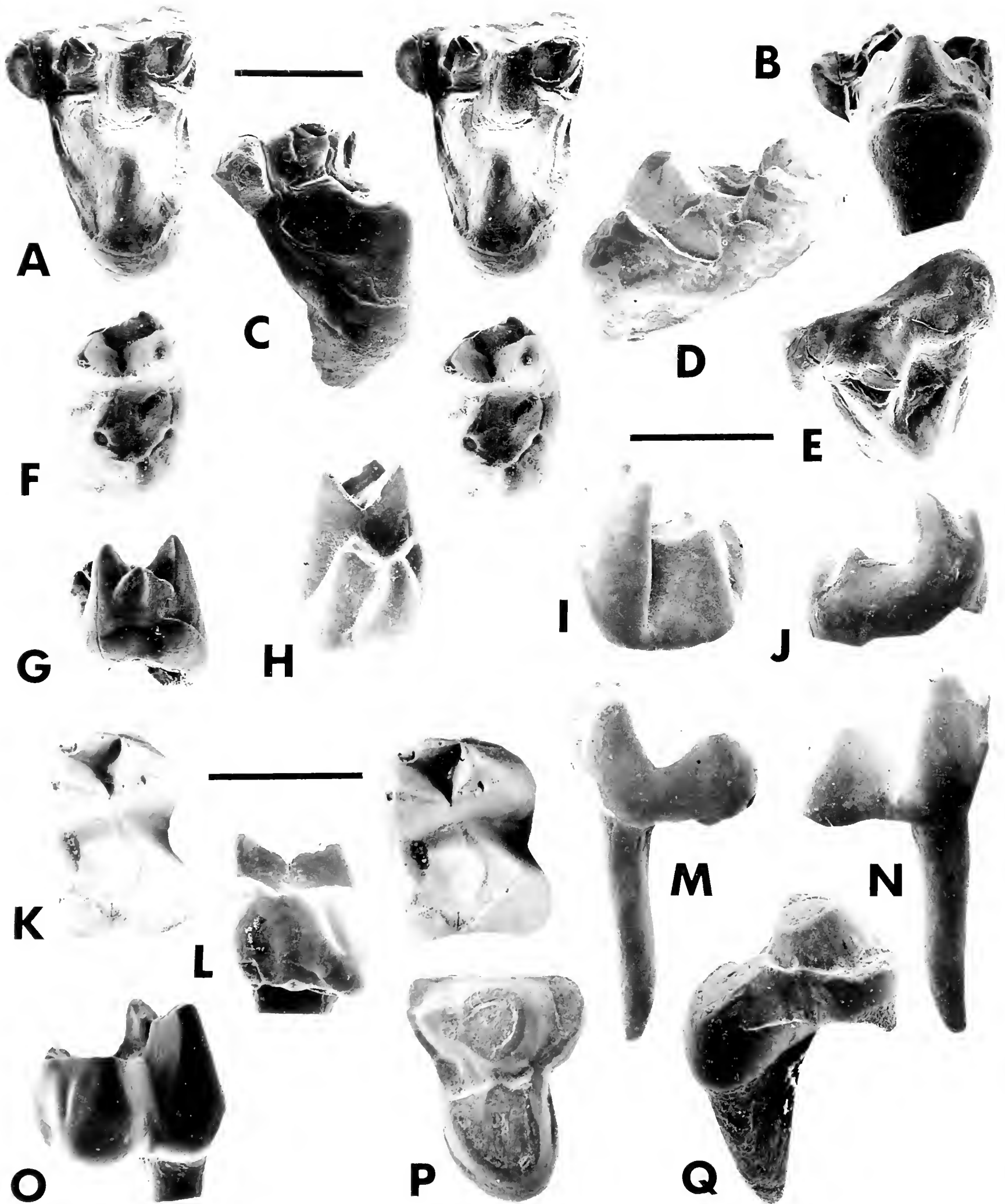
Fig. 14.—A–E. *Eoungulatum kudukensis*, n. gen. and sp., CCMGE 2/12455, holotype left M² in occlusal (A), lingual (B), anterior (C), posterior (D), and buccal (E) views. Occlusal view in A is stereopair. F–Q. cf. *Eoungulatum kudukensis*, n. gen. and sp. F–J. CCMGE 16/12953, left M₁ in occlusal (F), anterior (G), posterior oblique (H), buccal (I), and lingual (J) views. K–O. CCMGE 17/12953, right M₂ in occlusal (K), posterior (L), lingual (M), buccal (N), and posterobuccal (O) views. P, Q. CCMGE 35/12176, right P⁵ in occlusal (P), and anterior (Q) views. Occlusal views in A, F, and K are stereo pairs. Scales = 2 mm (upper scale corresponds to A–E; middle scale corresponds to F–J and M–Q; and lower scale corresponds to K–L).

Table 2.—Measurements (in mm) of Uzbek ungulatomorph lower dentitions. Italicized numbers are estimates. Daggers (†) indicate type specimens. Abbreviations are as follows: L, length; W, width; TRW, trigonid width; TAW, talonid width; TRL, trigonid length; TAL, talonid length.

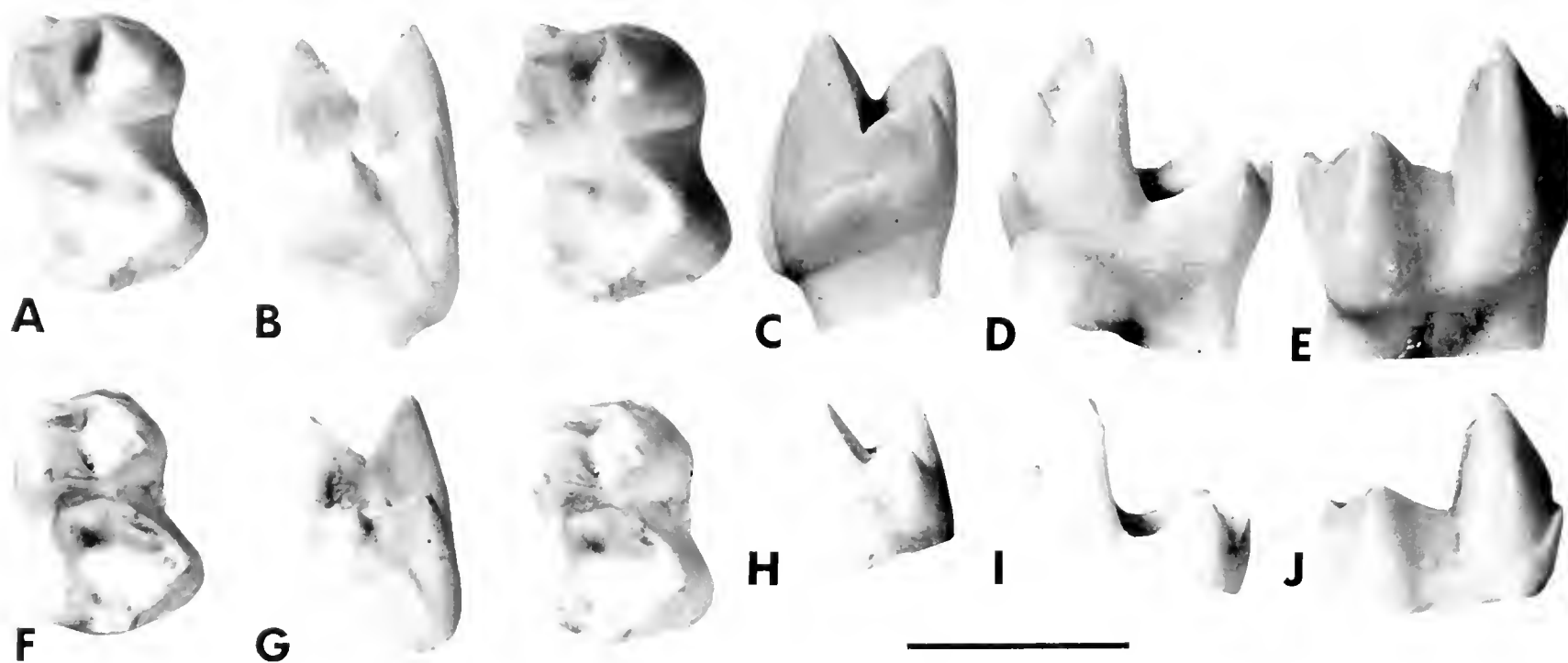| Specimen no.	P2 L	P2 W	P4 L	P4 W	P5 L	P5 W	M1 L	M1 TRW	M1 TAW	M1 TAL	M2 L	M2 TRW	M2 TAW	M2 TRL	M2 TAL	M3 L	M3 TRW	M3 TAW	M3 TRL	M3 TAL
Sorlestes budan																				
13/12953	—	—	—	—	—	—	2.4	1.5	1.6	1.3	—	—	—	—	—	—	—	—	—	—
1/12953	—	—	—	—	2.2	1.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2/12953	—	—	2.3	1.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3/12953	—	—	—	—	—	—	*2.4*	1.5	—	*1.3*	—	—	—	—	—	—	—	—	—	—
36/12000	—	—	—	—	—	—	—	—	—	—	2.4	1.8	1.8	1.1	1.3	—	—	—	—	—
†3/12176	—	—	—	—	—	—	—	—	—	—	2.8	1.8	1.8	1.3	1.5	—	—	—	—	—
4/12953	—	—	—	—	—	—	2.4	1.5	1.5	1.3	—	—	—	—	—	—	—	—	—	—
5/12953	—	—	—	—	—	—	2.4	1.5	1.6	1.3	—	—	—	—	—	—	—	—	—	—
14/12953	—	—	—	—	—	—	—	—	—	—	2.6	1.8	1.8	1.2	1.4	—	—	—	—	—
6/12953	—	—	—	—	—	—	—	—	—	—	2.6	1.7	1.7	1.2	1.4	—	—	—	—	—
15/12953	—	—	2.0	1.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2155-M-1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2.5	1.8	1.5	1.0	1.5
Averages	—	—	2.2	1.3	—	—	2.4	1.5	1.6	1.3	2.6	1.8	1.8	1.2	1.4	2.5	1.8	1.5	1.0	1.5
Kumsuperus avus																				
†13/11758	—	—	—	—	—	—	—	—	1.8	1.3	2.5	1.8	1.8	1.2	1.3	2.3	*1.5*	1.0	—	1.3
Aspanlestes aptap																				
7/12953	—	—	—	—	—	—	2.1	1.1	1.4	1.0	—	—	—	—	—	—	—	—	—	—
6/12176	—	—	1.6	0.9	—	—	—	—	—	—	—	1.6	1.6	1.0	*1.7*	1.9	1.4	1.1	0.9	1.0
†4/12176	—	—	—	—	2.1	1.0	2.1	1.5	1.5	1.1	2.2	1.6	1.6	0.9	1.2	2.0	1.3	1.2	0.8	1.2
69/12445	—	—	—	—	—	—	—	—	—	—	2.0	*1.5*	*1.5*	0.9	1.1	2.0	1.3	1.2	0.9	1.1
8/12953	—	—	—	—	—	—	—	—	—	—	2.0	1.6	1.6	—	1.1	—	—	—	—	—
9/12953	1.5	0.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Averages	—	—	1.6	0.9	2.1	1.0	2.1	1.3	1.5	1.1	2.1	1.6	1.6	0.9	1.3	2.0	1.4	1.2	0.9	1.1
cf. *Eoungulatum kudukensis*																				
16/12953	—	—	—	—	—	—	—	—	—	—	2.8	2.2	2.1	1.3	1.5	2.8	2.1	1.7	1.3	1.5
17/12953	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2.9	2.1	1.8	—	1.8
18/12953	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2.9	2.1	1.8	1.1	1.8
Averages	—	—	—	—	—	—	—	—	—	—	2.8	2.2	2.1	1.3	1.5	2.9	2.1	1.8	1.2	1.7

Fig. 15.—*Sorlestes budan* Nessov, 1985a. A–E. CCMGE 3/12176, cast of holotype right dentary with M_2 and alveoli for M_3 (not shown) in occlusal (A), posterior (B), anterior (C), lingual (D), and buccal (E) views. F–J. CCMGE 13/12953, cast of right M_1 in occlusal (F), posterior (G), anterior (H), lingual (I), and buccal (J) views. Occlusal views in A and F are stereopairs. Scale = 2 mm.

is the slightly smaller *Zhelestes temirkazyk*. This allocation cannot be eliminated as a possibility, but without stronger evidence, we prefer to refer both of these M_3s to cf. *Eoungulatum kudukensis*.

On the right M_2, CCMGE 17/12953, the only swelling of the crown seems to be at the base of the hypoconid (Fig. 14K–O). The other talonid cusps show some twinning. The paraconid is smaller than on either M_3, is slightly appressed to the metaconid, and is lingual to the midline of the tooth, but is not situated on the lingual margin of the molar. The pre- and postcingulids are very small and there are no labial or lingual cingulids. CCMGE 17/12953 shows some increase in the height of the trigonid and talonid, almost as much as on the M_3, CCMGE 16/12953, but more than on the other M_3, CCMGE 18/12953.

Sorlestes Nessov, 1985a

Type and Only Known Species.—*Sorlestes budan* Nessov, 1985a.

Distribution.—Late Cretaceous (late Turonian and Coniacian), western Uzbekistan.

Revised Diagnosis.—As for the type species.

Sorlestes budan Nessov, 1985a
(Fig. 10, 15, 16, 17)

Sorlestes budan Nessov, 1985a:14, pl. 2, fig. 13. Nessov and Kielan-Jaworowska, 1991:fig. 1; Nessov et al., 1994:18, pl. 1, fig. 7; Archibald, 1996b:1152, fig. 4C.
?*Zalambdalestes mynbulakensis* Nessov 1985b:212, pl. 2, fig. 2. Nessov et al., 1994:24, pl. 5, fig. 2.

Holotype.—CCMGE 3/12176, right dentary with M_2 and alveoli for M_3.

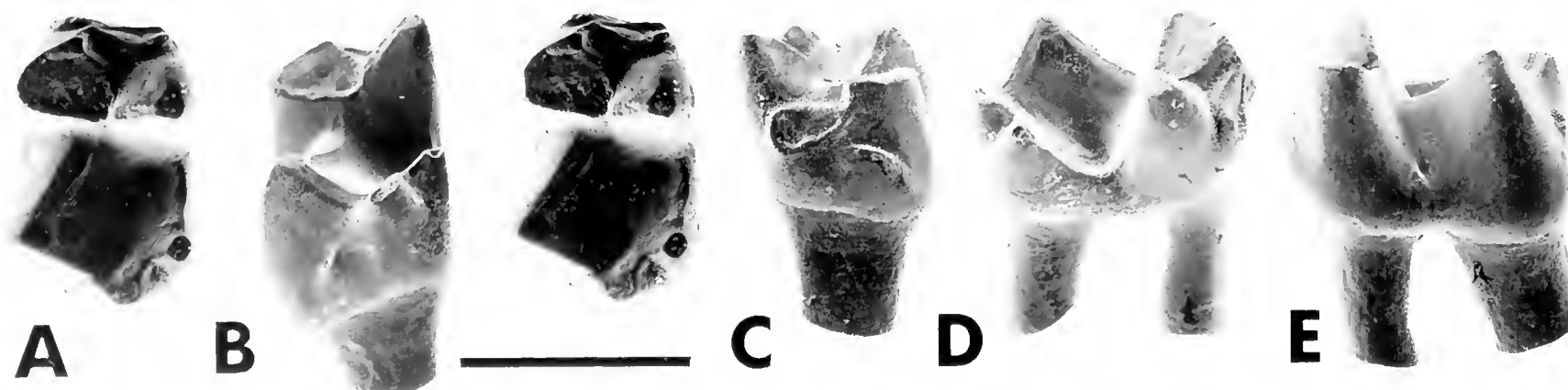*Type Locality.*—Locality CBI-14, middle part of

Fig. 16.—*Sorlestes budan* Nessov, 1985a. CCMGE 14/12953, left M_2 in occlusal (A), posterior (B), anterior (C), lingual (D), and buccal (E) views. Occlusal view in A is stereopair. Scale = 2 mm.

Bissekty Formation, Upper Cretaceous (Coniacian), Dzharakuduk, western Uzbekistan.

Referred Specimens.—CCMGE 2/12953, left P$_4$; CCMGE 5/12953, chemically weathered left M$_1$; CCMGE 13/12953, right M$_1$; CCMGE 3/12953, chemically weathered right M$_1$; CCMGE 14/12953, left M$_2$; CCMGE 6/12953, right M$_2$; CCMGE 36/12000 (type of ?*Zalambdalestes mynbulakensis*), left dentary with M$_2$ and alveoli for M$_3$; CCMGE 1/12953, left dentary with P$_5$, alveoli for M$_1$, roots of M$_2$, and alveoli for M$_3$; CCMGE 15/12953, left dentary with canine, two roots of P$_1$, two alveoli each for P$_{2-3}$, P$_4$; IZANUz P2155-M-1, left dentary with unerupted M$_3$.

Localities.—CCMGE 3/12953 is from locality CDZH-17a, lower part of Bissekty Formation, upper Turonian. CCMGE 5/12953 is from locality CBI-4b, middle part Bissekty Formation, Coniacian. CCMGE 36/12000, CCMGE 13/12953, CCMGE 14/12953, CCMGE 6/12953, CCMGE 1/12953, CCMGE 2/12953, and CCMGE 15/12953 are from locality CBI-14, middle part of Bissekty Formation, Coniacian. All localities are from the Upper Cretaceous, Dzharakuduk, western Uzbekistan.

Revised Diagnosis.—As in lower dentition of other "zhelestids": trigonid low relative to talonid, slight appression of paraconid and metaconid, pre- and postcingulids present, labial and lingual cingulids absent, entoconid and hypoconulid with some twinning. Lower dentition averages 22% larger (ranging from 0–31% for two measurements each on P$_{4-5}$, and for five measurements each on M$_{1-2}$) than smallest "zhelestid," *Aspanlestes aptap,* and 8% smaller (three measurements of M$_2$) in length and 20% smaller (two measurements of M$_2$) in width than the slightly larger cf. *Eoungulatum kudukensis.* The only possible autapomorphy is the intermediate size of this species, but as many as three species could be included.

Description.—A left dentary, CCMGE 15/12953, preserves a large, single-rooted canine, six alveoli or root fragments, and a two-rooted premolar. It appears that the canine may not be fully erupted. The premolar, which has some apical wear, is about 25% larger than (but similar in morphology to) the unworn penultimate premolar in the holotype dentary of *Aspanlestes aptap* (CCMGE 4/12176). Both are two-rooted, have a large protoconid, no paraconid, a cristid on the metaconid region, a small heel, and no cingulids. Both teeth are broadest just posterior to the protoconid, although CCMGE 15/12953 is slightly more bulbous, probably because of its slightly larger size. This dentary is too large to be referred to *Aspanlestes aptap,* but seems to be within the size range of *Sorlestes budan.* An isolated premolar (CCMGE 2/12953) is slightly larger than but comparable to the premolar in CCMGE 15/12953, both of which we feel are best regarded as P$_4$s (Fig. 10, 19D–F).

There are three specimens of M$_1$, four M$_2$s, including the holotype M$_2$, CCMGE 3/12176, and one M$_3$ assigned to *Sorlestes budan.* Two of the M$_2$s, including the type, are preserved in dentary fragments that also preserve the roots or alveoli for M$_3$. Based on these associations, plus differences in crown morphology and comparisons with the type dentary of *Aspanlestes aptap,* we are confident about our identifications as to locus of isolated molars assigned here to *Sorlestes budan.*

The M$_1$s average about 92% of the size of the M$_2$s except in the trigonid width of M$_1$, which is even smaller (about 83%). From what can be gleaned from the alveoli of M$_3$, this tooth was probably only slightly smaller than M$_1$ and M$_2$. Both M$_1$ and M$_2$ are similar in having a distinct precingulid, narrower postcingulid, and no labial or lingual cingulids. On both, the hypoconulid is slightly closer to the entoconid (twinning) than to the hypoconid. On M$_1$, the paraconid is nearer the anteroposterior midline than it is on M$_2$, in which it is distinctly more lingual. On M$_1$, the paraconid is less appressed to the metaconid than on M$_2$.

A left dentary fragment, IZANUz P2155-M-1, preserves the mandibular condyle, angular process, alveoli for M$_2$, and unerupted M$_3$ that has been exposed (Fig. 17A–D). This dentary fragment is of particular interest as it preserves both the mandibular condyle and the angular process. The dentary is dorsoventrally shallow, yet the preserved alveoli for M$_2$ are quite large (Fig. 17D), about the size for roots of M$_2$ in *Sorlestes budan* or *Aspanlestes aptap.* Such large alveoli relative to dentary size are often indicative of a young mammal. For example, compare the alveolar size relative to the size of the dentary in IZANUz P2155-M-1 versus CCMGE 23/12953 in Figure 19A. When originally collected, the dentary had a small foramen behind the second alveolus in IZANUz P2155-M-1 that was interpreted as the locular opening above an unerupted molar, which we surmised was M$_3$. When X-rayed, a tooth was detected. Most of the bone surrounding the tooth, which is clearly an M$_3$, was removed (Fig. 17B, D). In both the trigonid and talonid basins enamel had not completely formed, but enough is present to show "zhelestid" characteristics. The trigonid is slightly anteroposteriorly compressed and the hypoconulid and entoconid are somewhat twinned. This tooth is larger than M$_3$ in *Aspanlestes aptap,* but smaller than the M$_3$ tentatively referred to *Eoungulatum kudukensis* (Table 2). Also, if the M$_3$ in *Kumsuperus avus* is sufficiently preserved to indicate the true size of this tooth, it is similar in length but noticeably narrower than the M$_3$ in IZANUz P2155-M-1 (Table 2). If true, this suggests that *Kumsuperus,* with a reduced (especially narrowed) M$_3$, may be a senior generic synonym of *Parazhelestes,* at least one species of which (*P. robustus*) has a linguolabially narrow M^3.

The mandibular condyle in IZANUz P2155-M-1 is cylindrical, with the long axis labiolingually oriented; the labial end is higher (Fig. 17C). The condyle is posterior to the angular process and is just barely dorsal to the alveolar row. This is the presumed primitive position of the condyle in eutherians, if not therians. The well-preserved dentary of *Sorlestes kara* from Kazakstan described by Nessov (1993:pl. 1) preserves a condyle at or only slightly higher than that in IZANUz P2155-M-1. In earliest Tertiary ungulates (sensu stricto), such as *Protungulatum* or *Oxyprimus,* the mandibular condyle is dorsal to the occlusal surface of the tooth row.

The angular process in IZANUz P2155-M-1 is slightly inflected. A considerably more inflected angle is primitive for metatherians. The angle is unknown for most Late Cretaceous eutherians. For this reason we cannot assess whether the more modestly
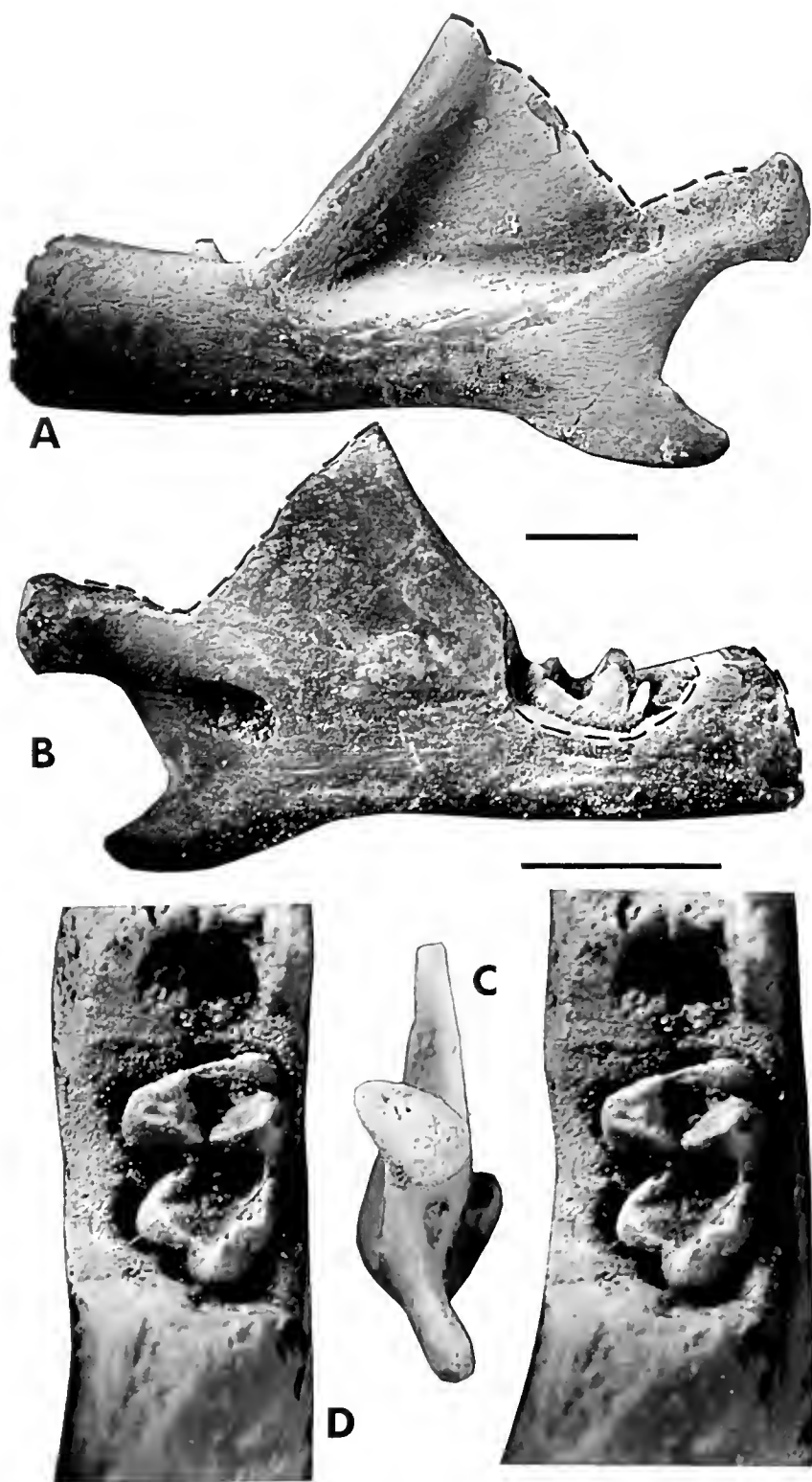
Fig. 17.—*Sorlestes budan* Nessov, 1985a. IZANUz P2155-M-1, left dentary preserving the mandibular condyle, angular process, posterior alveolus for M_2, and unerupted M_3 from which the surrounding bone has been removed. Views are buccal (A), lingual (B), posterior (C), and occlusal (D). Dashed lines indicate broken or removed surfaces. Occlusal view in D is stereopair. Scales = 2 mm (upper scale corresponds to A–C, lower scale corresponds to D).

inflected angle is an apomorphy of "zhelestids" or a larger clade of eutherians.

Discussion.—Figure 10 compares the type maxilla of *Zhelestes temirkazyk* and the fragmentary left dentary described above. As shown in this figure, the uppers and lowers are very similar in size, and the comparable teeth and alveoli align quite well. This fragmentary left dentary may belong to *Z. temirkazyk*. However, based on the material that we cur-

rently have available, it seems more prudent to refer this dentary fragment to *Sorlestes budan*, a taxon founded on lower teeth. The more recently named *S. budan* (founded on lower teeth) may prove to be a synonym of *Z. temirkazyk* (founded on upper teeth). Indeed, *S. budan* may include specimens belonging to as many as three taxa known from upper teeth: *Z. temirkazyk*, *Parazhelestes robustus*, and *P. minor*. Thus, we feel synonymization of *S. budan* with *Z. temirkazyk* is premature.

We are making the admittedly major assumption that the premolar count of five in the type specimen of *Zhelestes temirkazyk* (Fig. 9A, 10) and in a much larger edentulous dentary described below (Fig. 19A–C) is representative of all species we refer to "Zhelestidae." Given this assumption, the premolar preserved in CCMGE 15/12953 is P_4, as is an isolated premolar (CCMGE 2/12953) also referred to *Sorlestes budan*. This is also part of the basis for identifying the various submolariform upper premolars as P^5 and the two premolars in the type of *Aspanlestes aptap* (CCMGE 4/12176) as P_{4-5}.

Comments.—Nessov (1993:pl. 1, top three figures; Nessov et al., 1994:pl. 7, fig. 4) recently described a new species of *Sorlestes*, *S. kara*, based on a very well-preserved right dentary with P_5 and M_{1-3}. The specimen, CCMGE 106/12455, was recovered from a well core (Ashchikol locality) in south-central Kazakstan. It is believed to be early Turonian in age, which is slightly older than the late Turonian and Coniacian age advocated here for the "zhelestids" from the Dzharakuduk area in western Uzbekistan. Although the species is not included in our phylogenetic analysis because only the lower dentition is known, some characters distinguishing it from other taxa are included.

On the P_5 of *Sorlestes kara* compared to *Aspanlestes aptap*: the protoconid is higher, sharper, and more posteriorly curved; the metaconid is not developed; the precingulid on the labial side is stronger and bears a sharp cuspule; the postcingulid is much better developed; and the talonid basin is narrower labiolingually and strongly inclined lingually. Thus, P_5 in *S. kara* is not submolariform as it is in *A. aptap*.

M_2 in *Sorlestes kara* is similar to that in *S. budan*, but the latter is approximately 20% larger. Some differences are as follows: M_2 in *S. kara* has an incipient ectocingulid (absent in *S. budan*); the crown of M_2 in *S. kara*, especially the talonid, is not as high as in *S. budan*; the trigonid basin of M_2 in *S. kara* is shallower than in *S. budan*; and the paraconid of M_2 in *S. kara* is blade-like, but in *S. budan* the tip of the paraconid is slightly bulbous.
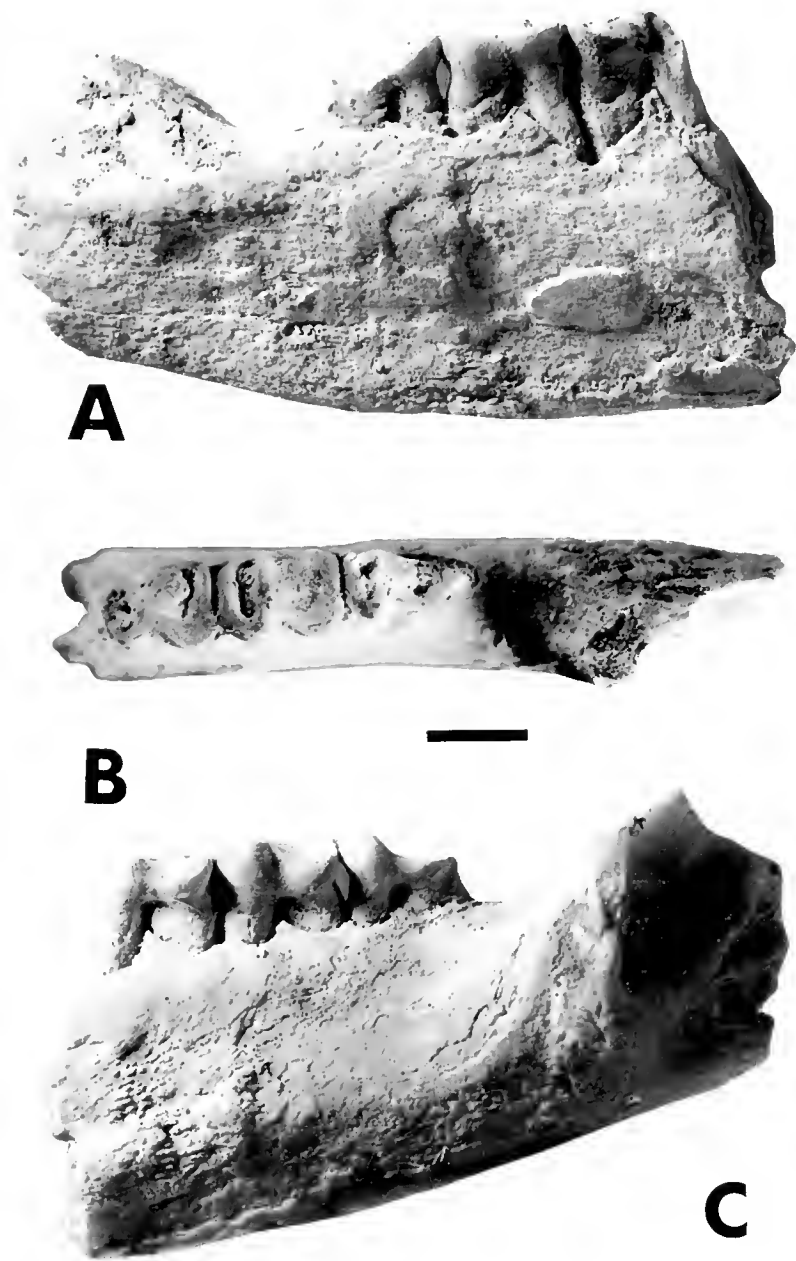
Fig. 18.—*Kumsuperus avus* Nessov, 1984*b*, nomen dubium. CCMGE 12/11758, holotype left dentary with heavily worn and slightly broken M$_{1-3}$ in lingual (A), occlusal (B), and buccal (C) views. Scale = 2 mm.

Kumsuperus Nessov, 1984*b*, nomen dubium

Type and Only Known Species.—*Kumsuperus avus* Nessov, 1984*b*, nomen dubium.

Distribution.—Late Cretaceous (Coniacian), western Uzbekistan.

Kumsuperus avus Nessov, 1984*b*, nomen dubium
(Fig. 18)

"Lower jaw of advanced placental mammal with M$_1$–M$_3$" Nessov, 1982:pl. 2, fig. 2.
Kumsuperus avus Nessov, 1984*b*:63, lower left, center left, and center images in figure. Nessov et al., 1994:14–15, pl. 2, fig. 1.

Holotype and Only Known Specimen.—CCMGE 12/11758, left dentary with heavily worn and slightly broken M$_{1-3}$.

Type Locality.—Locality CBI-4b, middle part of Bissekty Formation, Upper Cretaceous (Coniacian), Dzharakuduk, western Uzbekistan.

Discussion.—*Kumsuperus avus* Nessov, 1984*b* was based on a partial dentary with heavily worn M$_{1-3}$ from the Bissekty Formation in Dzharakuduk. It was originally figured by Nessov (1982:fig. 2a) as an "advanced placental mammal," and in 1984(*b*) he named and referred it to Eutheria incertae sedis. There is a slight suggestion of anteroposterior shortening of the trigonid in *Kumsuperus* compared to *Sorlestes budan*, but this can be attributed to either dental attrition or postmortem abrasion. When the lower teeth of these two taxa are plotted together (Fig. 6), and when their sizes are compared (Table 2), there is no detectable difference except for the linguolabial narrowing of M$_3$ in *K. avus*.

It may well be that *Kumsuperus avus* and *Sorlestes budan* are congeneric, if not conspecific. The problem is in attempting to determine which uppers and lowers go together. As already discussed, lowers of *Aspanlestes aptap* can be associated with considerable confidence with uppers previously attributed to *Zhelestes bezelgen*; and possible lowers of *Eoungulatum kudukensis* can be identified with less certainty. In the midsize range, we recognize three taxa of "zhelestids," *Zhelestes temirkazyk*, *Parazhelestes robustus*, and *Parazhelestes minor*. As noted above, the linguolabially narrow M$_3$ in *K. avus* is suggestive of possible synonymy between this taxon and *Parazhelestes*. It may ultimately be shown that some of the taxa discussed above are invalid or that different taxa are grouped under *Sorlestes budan*. For now, we think it is best to retain both *Sorlestes budan* and *Kumsuperus avus*, while recognizing that the latter taxon is questionable.

"Zhelestidae" genus and species indeterminate
(Fig. 19A–F)

A number of fragmentary teeth and edentulous dentaries may belong to "Zhelestidae." We briefly comment on only one of these specimens, CCMGE 23/12953, a right edentulous dentary with alveoli for canine (posterior portion only), P$_{1-5}$, M$_{1-3}$ (Fig. 19A–C). Based on size alone, CCMGE 23/12953 is very likely a "zhelestid" as no other mammal of this size is known from the Bissekty Formation. Also as discussed earlier, this dentary preserves alveoli for five premolars, of which P$_3$ appears to have been smaller than P$_2$ and P$_4$. This size pattern is found in at least one other "zhelestid" dentary that preserves teeth (Fig. 19D–F, CCMGE 15/12953, *Sorlestes budan*). The very deep excavation of the masseteric fossa (Fig. 19B) may also be characteristic of "zhelestids."

NORTH AMERICAN "ZHELESTIDS"

Fox (1989) named *Alostera saskatchewanensis* based on material from the Scollard and Frenchman formations of Alberta and Saskatchewan, Canada, and the Hell Creek Formation, Montana, U.S.A. There is universal agreement that the localities in the Scollard Formation are latest Cretaceous (Lancian) in age. More recently studied localities in the Frenchman Formation are of less certain age, although Fox (1995) argued that, based on palynological data, these sites are also latest Cretaceous in age. The site in Montana that yielded specimens of *Alostera saskatchewanensis* is Bug Creek Anthills, which (as discussed in the Introduction) we regard as probably lying within the lowermost Paleocene Tullock Formation rather than the latest Cretaceous Hell Creek Formation.

Alostera saskatchewanensis is a rather curious species. Fox (1989) noted similarities with *Gypsonictops* and *Purgatorius*. Although not denying these similarities, we feel that the most likely evolutionary affinities are with Ungulatomorpha, more specifically "zhelestids." *Alostera* is similar to "zhelestids" and some other Late Cretaceous eutherians in having only a slight expansion of the protocone and in maintaining large conular wings, yet it is very much like early Tertiary archaic ungulates in

having even greater reduction of the stylar shelf and accompanying cuspules, loss of parastylar groove and reduction to one parastylar cusp, and a metacingulum formed by the continuation of postmetaconule crista onto the metastylar lobe. These character states suggest that *Alostera* could simply be an odd archaic ungulate, but our phylogenetic analysis (presented next) suggests that it is an ungulatomorph of uncertain affinities. The variable presence of a distinctive mesostylar cusp is probably autapomorphic for this taxon (Fig. 22H).

Fox described and figured (1989:pl. 3, fig. 8) a lower molar (UALVP 3685) that he referred to *Alostera saskatchewanensis*. This tooth is almost identical in size and is similar in morphology to the M_1 of *Sorlestes budan* described earlier and illustrated in Figure 15F–J. Fox (1989) noted that the hypoconulid was equidistant from the entoconid and hypoconid. The tip of the hypoconulid is broken, however, so that it is difficult to say whether or not there would have been some slight twinning of hypoconulid and entoconid. Another possibly significant way in which the M_1 of *A. saskatchewanensis* differs from that of *Sorlestes budan* is the presence of a slightly larger and more cusp-like paraconid in the former species. It may also be less appressed to

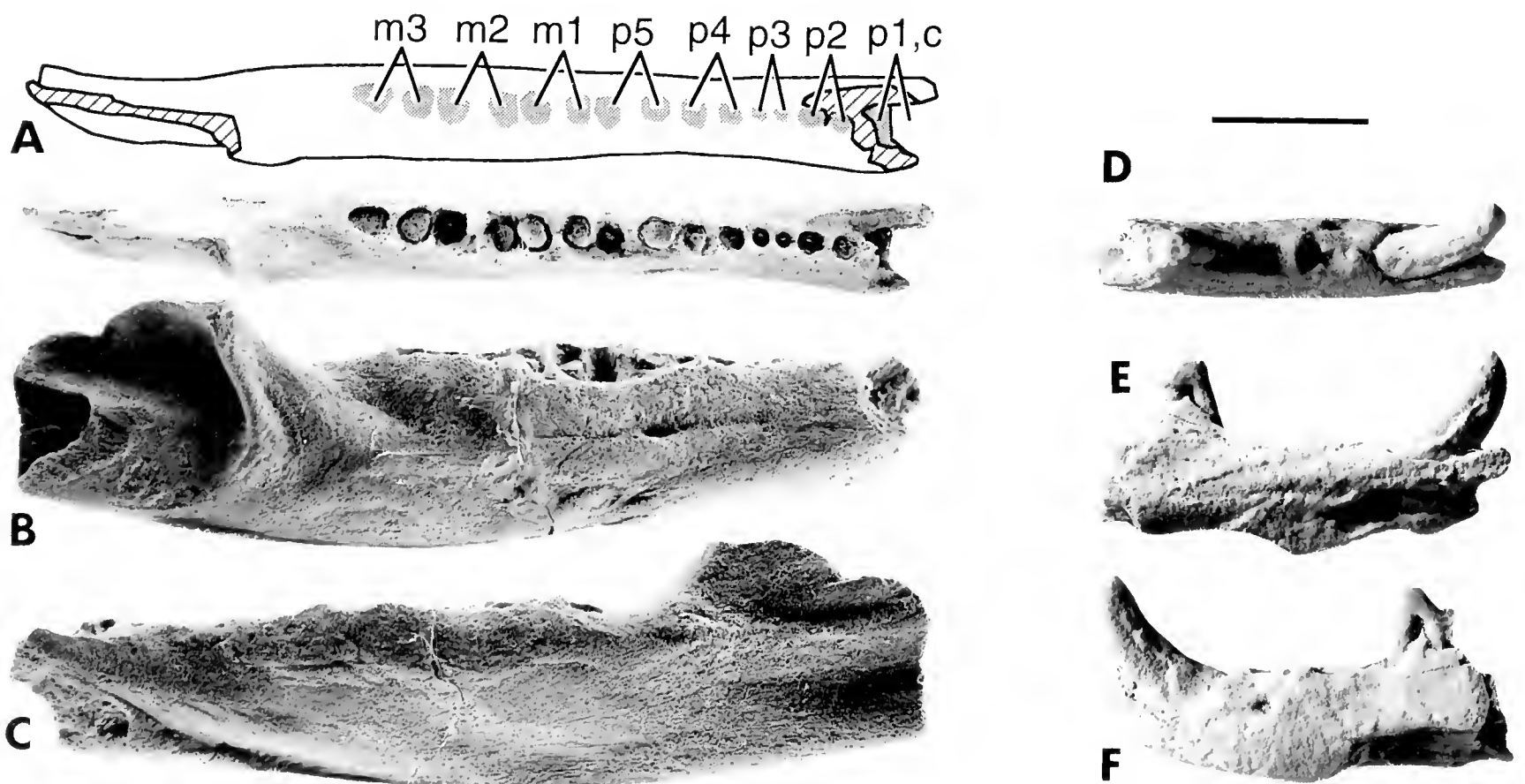
Fig. 19.—Dentary fragments of "zhelestids." A–C. CCMGE 23/12953, right edentulous dentary preserving alveoli for C_1–M_3 in occlusal (A), buccal (B), and lingual (C) views. D–F. CCMGE 15/12953, *Sorlestes budan*, left dentary preserving C_1, two roots of P_1, two alveoli each for P_{2-3}, and crown of P_4 (alveoli as marked in Figure 10). Scale = 5 mm.

cf. *Eoungulatum kudukensis*
CCMGE 35/12176

Eoungulatum kudukensis
CCMGE 2/12455

Parazhelestes robustus
CCMGE 70/12455

Zhelestes temirkazyk
CCMGE 10/12176

Parazhelestes minor
CCMGE 11/12176
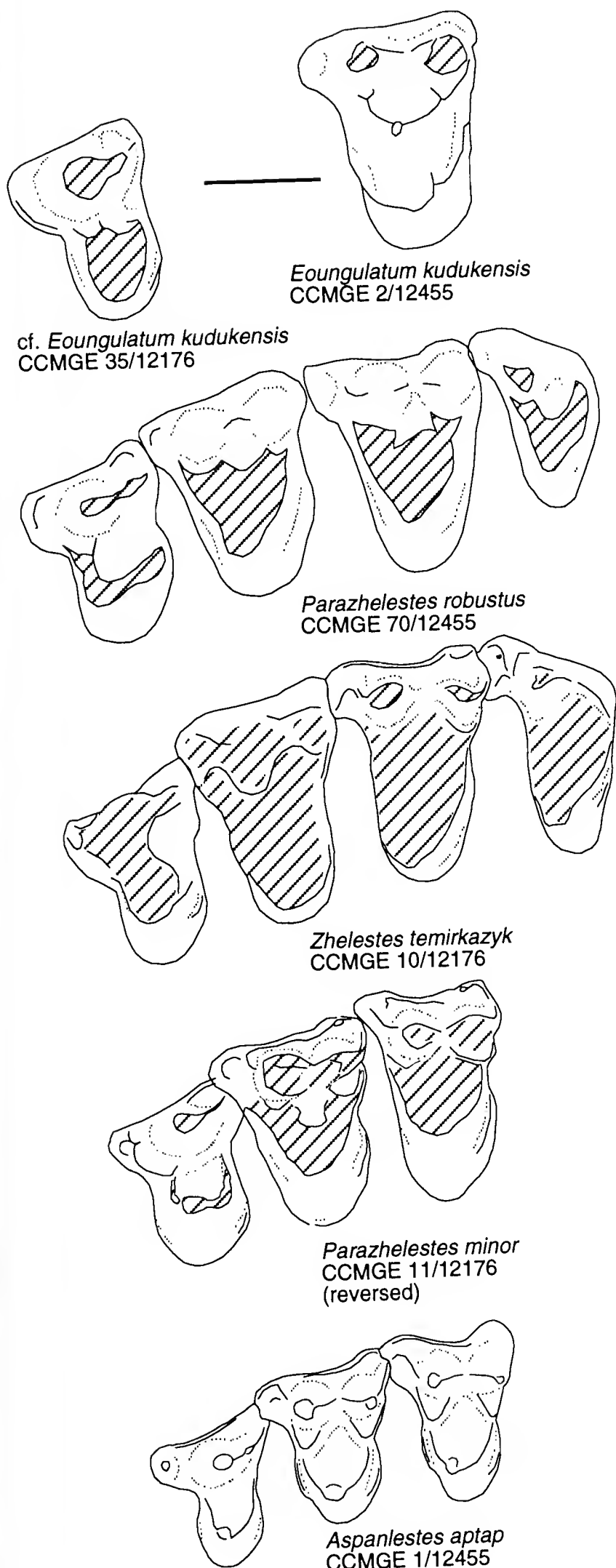(reversed)

Aspanlestes aptap
CCMGE 1/12455

Fig. 20.—Comparative occlusal views of the upper left dentitions of zhelestids (except for *Parazhelestes minor* and cf. *Eoungulatum kudukensis*, which are reversed from the right side). The

the metaconid in the former species. However, because the metaconid is missing in UALVP 3685, this cannot be properly assessed. Another lower molar (SMNH P1927.454) from the latest Cretaceous of Saskatchewan was referred to *A. saskatchewanensis* by Fox (1989), and was mentioned and figured by Storer (1991). Although similar in length to M_1s of *S. budan*, it is distinctly narrower. Finally, Fox (1989) noted that a dentary with a complete lower molar and part of a second that was the basis of the species *Paranyctoides megakeros* from the "Mesaverde" Formation (Judithian) of Wyoming (Lillegraven and McKenna, 1986) likely belongs to a species of *Alostera*.

Avitotherium utahensis (Fig. 22G) is from the mid-Campanian (Judithian) Kaiparowits Formation of south-central Utah (Cifelli, 1990). Cifelli (1990) noted its similarities to both *Paranyctoides* and *Alostera*. Especially of relevance here is his statement (1990:357) that *Avitotherium* resembles *Alostera* in the "reduction of labial shearing structures, with concomitant development of crushing and grinding wear patterns (also seen in *Purgatorius* and *Protungulatum*)." We agree with this as well as his other assessments of *Avitotherium*, but note that (although from separate continents and separated by as much as 10 million years) *Avitotherium* and *Aspanlestes aptap* show even greater similarities (both primitive retentions and apomorphies), including two cuspules in the parastylar region. Comparing the types of *A. utahensis* (MNA V4650; Cifelli, 1990:fig. 6A, B) and *A. aptap* (CCMGE 1/12455, Fig. 7A), the only differences are a slightly smaller size, slightly more lingually placed protocone, and a closer approximation in size for the paracone and metacone in *A. utahensis*. Even the slightly more lingual placement of the protocone is duplicated in other upper molars we refer to *A. aptap*. These taxa may eventually be synonymized at least at the generic level, but given the fragmentary nature of the material we avoid such a step at this time.

Cifelli (1990:fig. 6) also figured a lower molar (M_1 or M_2, OMNH 20424) and a lower premolar in a dentary fragment (P_3, OMNH 20532), both of which he assigned to *Avitotherium utahensis*. The M_x is very close in length to both M_1s and M_2s

←

bottom two dentitions preserve P^5–M^2, the middle two preserve P^5–M^3, and the uppermost is isolated P^5 and M^2. Diagonal lines indicate areas of dental attrition. Scale = 2 mm (see Table 3).

referred to *Aspanlestes aptap*. With its slightly larger and slightly more labially placed paraconid, the trigonid of M$_x$ referred to *A. utahensis* resembles the trigonid of M$_2$s more than the trigonid of M$_1$s assigned to *A. aptap*. The widths of both the trigonid and talonid of M$_x$ are closer to the comparable widths seen in M$_1$s referred to *A aptap*. The two greatest differences between the M$_x$ of *A. utahensis* and M$_1$s or M$_2$s of *A. aptap* are a noticeably shorter talonid and an apparent lack of twinning of the entoconid and hypoconulid on the M$_x$ of *A. utahensis*. P$_3$ in the dentary fragment referred to *A. utahensis* by Cifelli (1990) appears to have been larger than the fragmentary tooth preceding it in the dentary, identified as P$_2$ by Cifelli (1990). No complete P$_3$s of any "zhelestids" are known, but what evidence is available strongly argues that this two-rooted tooth is smaller than P$_2$. It is possible that the tooth identified as P$_3$ in Asian "zhelestids" has been lost in *A. utahensis*, and thus the tooth identified as P$_3$ in *A. utahensis* is homologous with the tooth identified as P$_4$ in Asian "zhelestids." Even if this highly speculative homology is correct, the premolar of *A. utahensis* has a more basined talonid (with two cusps) compared to a more trenchant talonid on P$_4$ of *A. aptap*. Further, the premolar of *A. utahensis* has no suggestion of a metaconid, while the P$_4$ of *A. aptap* has a swelling in this region (Fig. 7).

An upper molar, either M^1 or M^2, figured and briefly described as cf. *Paranyctoides* by Montellano (1992) from the middle Campanian (Judithian) Judith River Formation of north-central Montana is referable to *Avitotherium*, or possibly even *Aspanlestes*. Except for being 0.1 mm longer, this tooth is within the size range of M^1 of *Aspanlestes*, but is slightly larger than upper molars of *Avitotherium*. Based on Montellano's drawing of the specimen (1992:fig. 29), it differs from M^{1}s of *Aspanlestes* only in having a slightly anteroposteriorly wider protocone, a possibly narrower postcingulum (unless it is broken), and more widely spaced preparastyle and parastyle.

Gallolestes pachymandibularis Lillegraven, 1976 is based on three dentary fragments and two isolated molars collected from the "El Gallo Formation" in the state of Baja California del Norte, Mexico. The teeth known in the type specimen (LACM 42633) have been identified tentatively as P$_{3-4}$ and M$_{1-3}$. Other material confirms the relative positions of these teeth. The tentative nature of the identification centers on the tooth identified as P$_4$. The complete trigonid is molariform with three cusps,
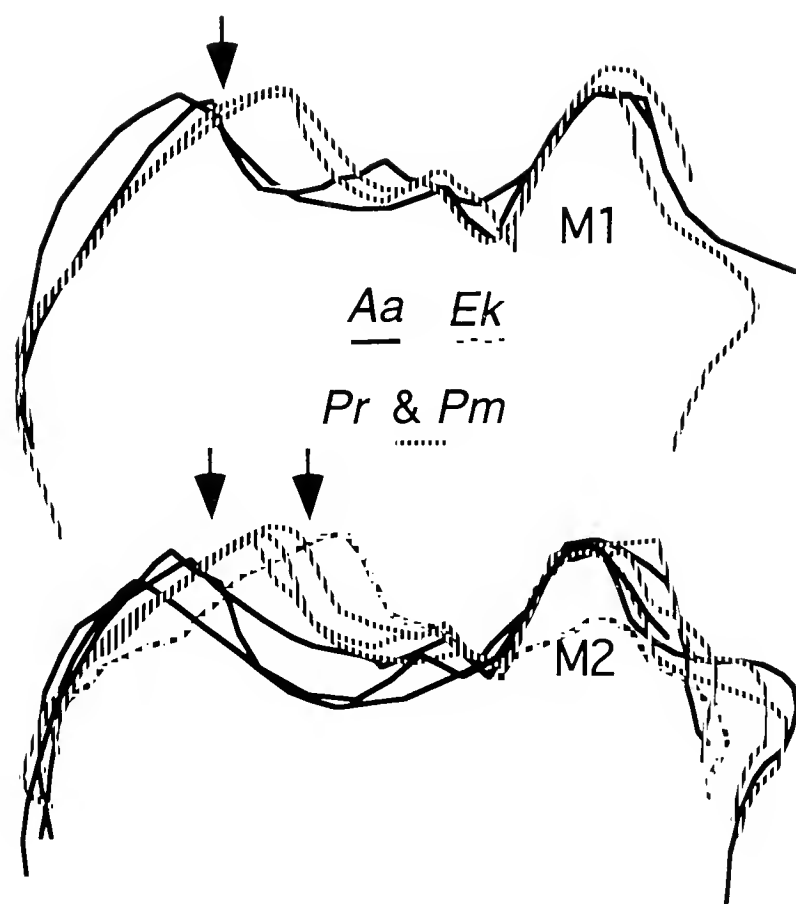

Fig. 21.—Posterior outlines of relatively unworn M^{1}s and M^{2}s of *Aspanlestes aptap* (*Aa*), *Eoungulatum kudukensis* (*Ek*), *Parazhelestes robustus* (*Pr*), and *Parazhelestes minor* (*Pm*). All molars shown as if from left side. Width is standardized so that the lingual margin and the outline of the metacone are approximated on all the molars. Arrows delimit the three states (different line patterns) in the labial shift of protocone (Table 3, character 2).

and although the talonid is mostly missing, what remains suggests a basined structure as seen on molars (Lillegraven, 1976). Lillegraven (1976) reviewed most if not all the likely possibilities, appearing to favor the interpretation that the tooth is a molariform P$_4$ in a eutherian insectivore, unlike known Cenozoic taxa. Clemens (1980) followed Lillegraven's assignations of teeth, but concluded that *Gallolestes* was not clearly a eutherian or metatherian, but was probably a separate derivative of a metatherian–eutherian grade mammal. Butler (1977, 1990) argued that the tooth in question is a "molariform milk-molar." This seems reasonable especially because the tooth is more heavily worn than the succeeding three "molars." As Clemens (1980) pointed out, retention of the last deciduous premolar until the M$_3$ is erupted is quite unusual. Butler (1990) responded that a specimen of *Barunlestes* retains the last two deciduous premolars (with an unerupted permanent premolar below the last deciduous premolar) although the M$_3$ is erupted. This seems the most plausible explanation. Perhaps Late Cretaceous eutherians in general retained their deciduous premolars longer.

Given this interpretation of "P$_4$" as a deciduous

P_4 in *Gallolestes pachymandibularis*, the remainder of the dentition looks remarkably like that of a "zhelestid," hence our assignment of this taxon to this group. Expanding on Lillegraven (1976), Clemens (1980) listed a number of characters of *Gallolestes* that he regarded as apomorphies relative to other Late Cretaceous eutherians, but which are also shared with zalambdalestids: 1) trigonid of last premolar molariform; 2) paraconid on molars slightly labial, close to metaconid, and trigonid canted anteriorly; 3) molar talonids broad; 4) hypoconulid and entoconid approximated; 5) M_3 hypoconulid nearly medial and salient; and 6) trigonid of M_3 narrower than talonid of M_2. The P_5 in "zhelestids" is not quite as molariform as the possibly comparable "P_4" in *Gallolestes* but, as noted in the previous paragraph, we regard this tooth in *Gallolestes* as deciduous P_4.

A second species of *Gallolestes*, *G. agujaensis*, was named by Cifelli (1994) based on six lower molars and molar fragments, and three upper molar fragments from the Judithian Terlingua local fauna, Big Bend area, Texas. Cifelli (1994) indicated that *G. agujaensis* is 40% smaller, has more delicately constructed molar cusps, and has more vertically developed shearing surfaces than *G. pachymandibularis*. Otherwise, *G. agujaensis* is similar to *G. pachymandibularis*. If correctly assigned, the upper molar fragments that he includes are the first known uppers for a species of *Gallolestes*. As noted by Cifelli (1994), the two lingual fragments of M^1 or M^2 possess pre- and postcingula, although a distinct hypocone is not present on either. He did not comment on the presence or absence of conular wings; further, this area is not well preserved on the specimen figured by Cifelli (1994:fig. 9F). The labial part of the M^3 he referred to *G. agujaensis* (Cifelli, 1994:fig. 9G) cannot be compared easily with the two worn M^3s known for Asian "zhelestids," although what can be seen does not argue against "zhelestid" affinities. Too little is known to provide further comparisons of the upper molars in these taxa.

The following characters found in both species of *Gallolestes* appear to be derived for "zhelestids" (including *Gallolestes*) relative to zalambdalestids: lower trigonid relative to talonid, overall lower crown height, relatively larger talonid basin, and possibly greater hypoconulid–entoconid twinning. Relative to zalambdalestids, *G. pachymandibularis* also has a greater robustness of the dentary (dentary unknown for *G. agujaensis*) and is larger. *Gallolestes* and "zhelestids" also retain two characters that appear to be primitive relative to conditions in zalambdalestids. These are less anteroposterior compression of the trigonid and less size reduction of M_3 relative to M_2.

?UNGULATOMORPHA: A QUESTIONABLE NORTH AMERICAN "ZHELESTID"

Emry et al. (1981) described a fragmentary molar preserving the labial half of the trigonid and the complete talonid from the upper Santonian Eutaw Formation in the vicinity of Vinton Bluff, Mississippi, U.S.A. The authors argued that, based on what could be determined, the specimen resembled the archaic ungulate *Protungulatum* to a greater extent than either *Gallolestes* or *Purgatorius*. The trigonid is low relative to the talonid, the talonid is quite broad, the entoconid and hypoconulid are somewhat approximated, and the tooth is mildly bulbous. The tooth is only slightly larger than M_2s we assign to cf. *Eoungulatum kudukensis*. This tooth is probably a "zhelestid."

EUROPEAN "ZHELESTIDS"

Gheerbrant and Astibia (1994) named *Lainodon orueetxebarriai* from the Maastrichtian locality of Laño in the Basque region, Spain. They compared it with *Labes quintanillensis* Sigé (*in* Pol et al., 1992) from the Maastrichtian locality of Quintanilla del Coco in northern Spain and *Labes garimondi* Sigé (*in* Pol et al., 1992) from the Campanian locality of Champ-Garimond near the village of Fons in southern France. *Lainodon orueetxebarriai* is based on two possible M_1s, one possible M_2, a P_2 or P_3, and two molar talonids (Gheerbrant and Astibia, 1994; Gheerbrant, personal communication). *Labes quintanillensis* is based on a left lower molar, identified as M_3, and a fragment of the lingual portion of M_x. *Labes garimondi* is based on two lower molars, one of which had been referred to as the "Champ-Garimond tooth" (Ledoux et al., 1966) prior to its formal systematic description, and the second of which was reported and figured by Pol et al. (1992) at the time *Labes garimondi* was named.

In their discussion of these three taxa from Spain and France, Gheerbrant and Astibia (1994) con-
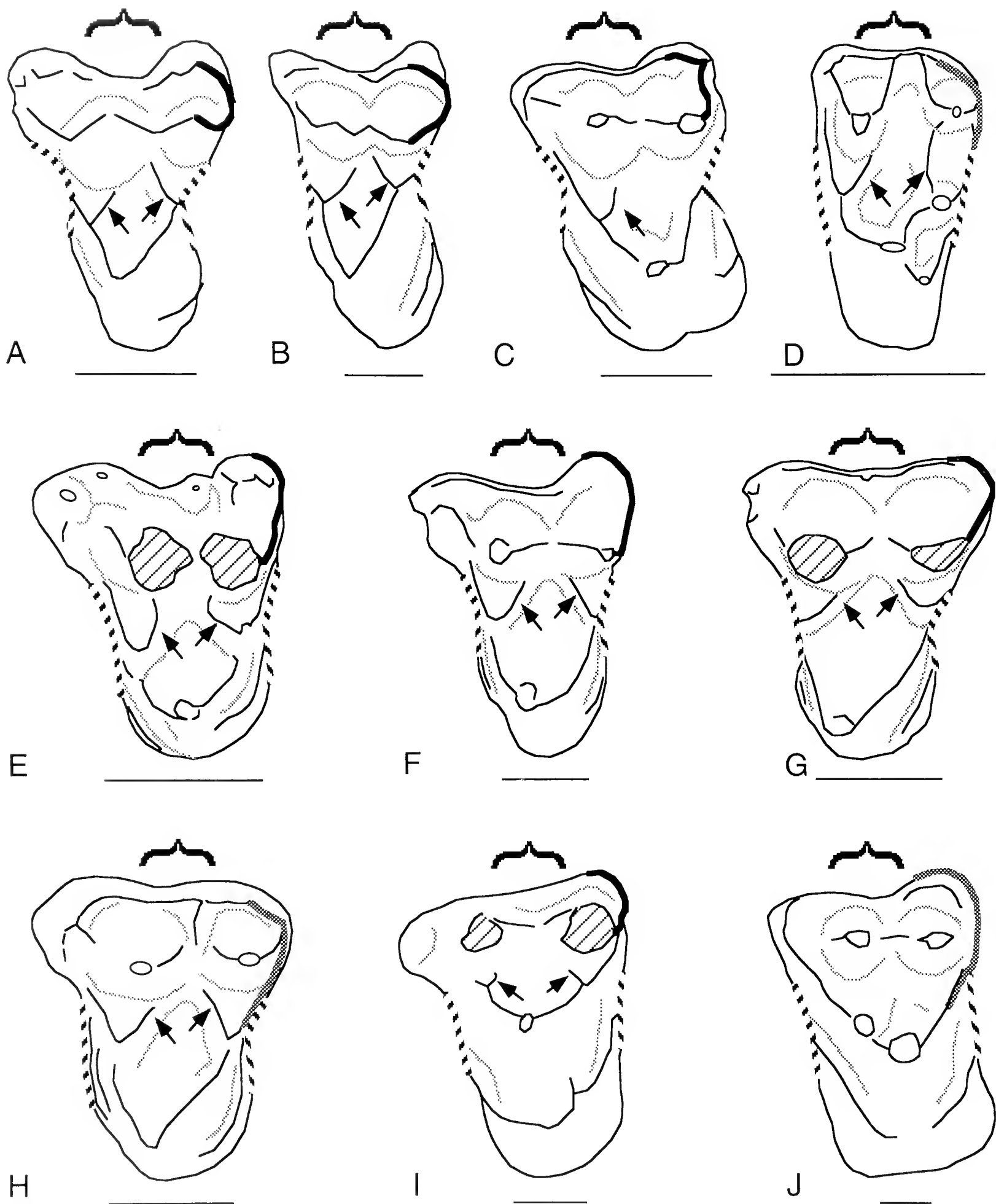
Fig. 22.—Occlusal views of M¹s or M²s (all shown as if from left side). A. *Kennalestes gobiensis* M². B. *Gypsonictops illuminatus* M². C. *Purgatorius unio* M². D. *Tribosphenomys minutus* M¹. E. *Paranyctoides* sp., cf. *P. maleficus* M¹ or M². F. *Aspanlestes aptap* M². G. *Avitotherium utahensis* M¹ or M². H. *Alostera saskatchewanensis* M¹. I. *Eoungulatum kudukensis* M². J. *Protungulatum donnae* M². Molars drawn at same width. Scales (horizontal lines) = 1 mm. Sketches are after figures from the following sources, supplemented by casts or specimens: A–C, J (Kiclan-Jaworowska et al., 1979); D (Meng et al., 1994); E (Montellano, 1992); G (Cifelli, 1990); and H (Fox, 1989). Note the following character states: ectoflexus (bracket) ranges from deep to shallow (e.g., A vs. D, respectively); post-metacrista continuous with metastylar area so that metacingulum is formed only by the postmetaconule crista (thick black line) or metacingulum formed by postmetaconular crista continuing onto metastylar region (thick gray line) (e.g., F vs. J, respectively); degree of waisting of molar occlusal outline (thick, diagonally hatched lines) ranges from very waisted to only slightly or not waisted (e.g., A vs. I, respectively); internal conular cristae (arrows) are pronounced to weak or absent (F vs. J, respectively) (see Table 3).

cluded that they appear to form a suprageneric group showing affinities with the mixotheridians ("zhelestids" as used here), as characterized by Nessov (1985a). Although Gheerbrant and Astibia (1994) entertained several phylogenetic hypotheses for these European Cretaceous eutherians, such as derivation from North American *Gypsonictops* or a sister group relationship to zalambdalestids, their favored hypothesis advocated a close relationship with "zhelestids," essentially in the sense we use the group here. Earlier, Butler (1990) thought that the "Champ-Garimond tooth," now *Labes garimondi*, was probably a first molar similar to *Gallolestes* and his "group d," which, along with several other taxa, includes what we call "zhelestids." Sigé (*in* Pol et al., 1992) argued that *Labes* has closer phylogenetic affinity to archaic ungulates ("condylarths") than does North American *Protungulatum donnae*. Although *P. donnae* may be more advanced in some characters than taxa such as the similarly aged North American *Oxyprimus* sp., (e.g., *P. donnae* has more bulbous teeth, has a larger and more lingual paraconid, has little or no metaconid on the ultimate premolar; see Luo, 1991), there is no doubt that it is an archaic ungulate showing closer affinities to other ungulates than does *Labes*.

The three European taxa are very similar to "zhelestids," notably in having an expanded talonid and greater tendency for bunodonty. Gheerbrant and Astibia (1994) noted that *Lainodon* and *Labes* differ from "zhelestids" in having: more massive cusps, less difference in trigonid and talonid height (the trigonid is lower), the paraconid transversely reduced, the precingulid large and high on the trigonid contacting the midpoint of the paracristid, the labial surface of the protoconid with a slightly concave profile, the postcingulid absent, and noticeably less overhang (exodaenodonty) of the lower labial margin of the molar crown. In comparing casts and/or specimens of *Lainodon*, *Labes*, and Asian "zhelestids," E. Gheerbrant and D. Archibald observed that *Lainodon* and *Labes* differ from Asian "zhelestids" in having a more lingual placement of the paraconid, which aligns this cusp and the metaconid, and in having the paraconid and metaconid more rounded than transversely elongate in occlusal view. The possible phylogenetic significance of these differences are under study by E. Gheerbrant, but they suggest that *Lainodon* and *Labes* form a clade, either within "Zhelestidae" or as a very close sister clade.

TAXA REMOVED FROM "ZHELESTIDAE"

Wang (1995) described a new middle Paleocene mammal, *Wania chowi*, from the Qianshan Basin, Anhui Province, China, which he referred to Mixotheridia, Zhelestidae. The taxon was based on dentaries and maxillary fragments of the same individual. The upper molars do show some similarities to taxa here assigned to "Zhelestidae," such as narrowing of the stylar shelf, increase in the linguolabial dimension of upper molars, and reduction of M^3 and M_3 (*Parazhelestes robustus* and *Kumsuperus avus*). Aside from the reduction of M^3 and M_3, which is not found in all "zhelestids," the other two resemblances are widespread in Late Cretaceous and early Tertiary mammals. Thus, we see no basis to suggest that *W. chowi* is a "zhelestid." This taxon does, however, bear some resemblance to anagalidans, and it is to this group that *W. chowi* may be related. The second author (J.D.A.) was kindly shown the specimens of *Wania chowi* by its describer, Wang Yuanqing. This brief examination confirmed our earlier assessment that *Wania chowi* is not a "zhelestid."

As recently as 1994 Nessov retained *Taslestes inobservabilis* in "Zhelestidae" with reservations (Nessov et al., 1994). As noted earlier in this paper, we remove *T. inobservabilis* from "Zhelestidae." At the time of his death, the first author (L.A.N.) was working on manuscripts dealing with the non-"zhelestid" therians from southwestern Asia, including Uzbekistan. This unpublished work included more complete argumentation for the removal of *T. inobservabilis* from "Zhelestidae." The second and third authors have not seen these manuscripts; thus, the following comments, although probably agreeing with Nessov's unpublished assessments, are ours alone.

Taslestes inobservabilis is based on a right dentary preserving M_2 and alveoli for M_1 and M_3 from the lower part of the Bissekty Formation (locality CDZH-17b) at Dzharakuduk, the general area from which most "zhelestids" have been recovered. The M_2 of *T. inobservabilis* is only about 60% of the size of M_2 in the smallest Asian "zhelestid," *Aspanlestes aptap*. In proportions of the crown the two species are similar, except that the greatest width of the M_2 (especially on the talonid) of *T. inobservabilis* is at the base of the crown, while the occlusal surface of the M_2 of *A. aptap* is relatively more
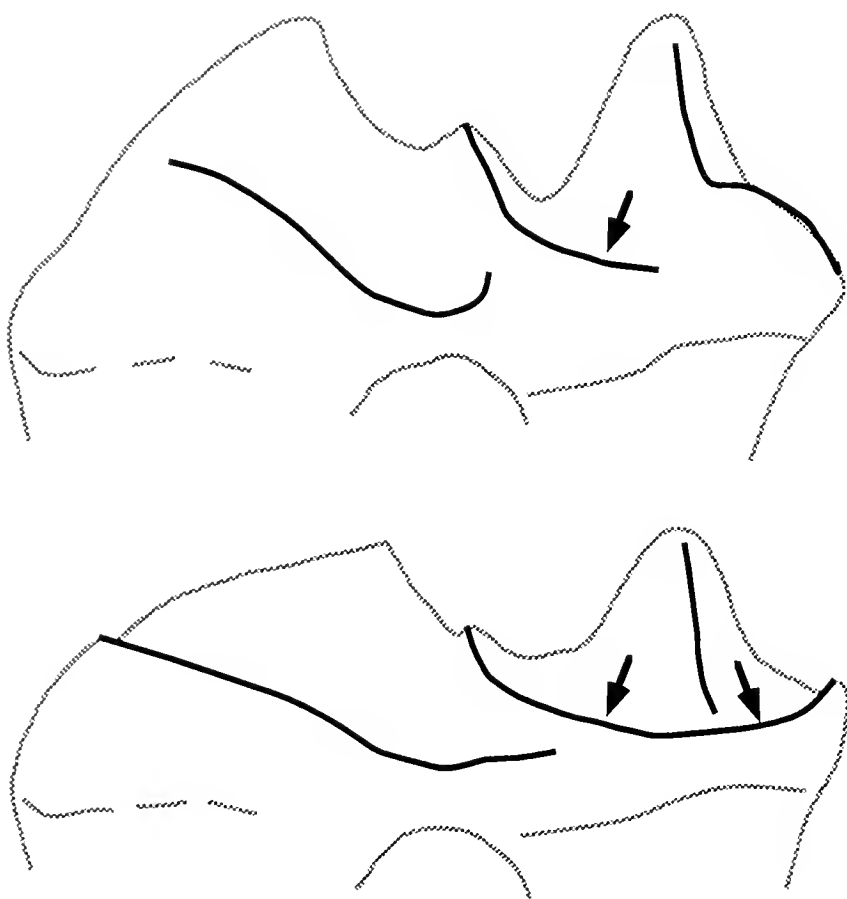
Fig. 23.—Upper molars of a generalized "zhelestid" (above) and an archaic ungulate (below) in posterior view. In "zhelestids" and Late Cretaceous eutherians, the postmetaconule crista forms the metacingulum (arrow), while in ungulates the metacingulum is formed by the postmetaconule crista continuing onto the metastylar lobe (arrows) (see Table 3, character 4).

expanded. Further, the paraconid is larger and less appressed to the metaconid on the M_2 of *T. inobservabilis* than is the case in *A. aptap*. The degree of entoconid/hypoconulid twinning is comparable in both species. Although these differences are relatively minor, they are sufficient to exclude *T. inobservabilis* from "Zhelestidae" at the present time. A partial skull with lower jaws recovered at locality CBI-5a at Dzharakuduk may be congeneric or conspecific with *T. inobservabilis*, and thus may provide more answers about the affinities of this taxon.

(Grandorder) Ungulata Linnaeus, 1766

Included Taxa.—The paraphyletic assemblage "Condylarthra" that is here informally termed archaic ungulates (Archibald, in press), the South American native ungulates listed by Cifelli (1993, i.e., Litopterna, Astrapotheria, Notoungulata, Pyrotheria, and Xenungulata), Desmostylia, Embrithopoda, Artiodactyla, Cetacea, Hyracoidea, Perissodactyla, Proboscidea, Sirenia, and questionably Tubulidentata. Following Lucas (1993), taxa explicitly excluded from Ungulata (sensu stricto) are Pantodonta, Tillodontia, and Dinocerata.

Distribution.—See distribution under Ungulatomorpha.

Definition.—All ungulates sharing a more recent common ancestor with each other than with any other eutherians. This is a node-based phylogenetic definition following the protocol suggested by de Queiroz and Gauthier (1990).

Diagnosis.—In addition to character states shared with other Ungulatomorpha ("zhelestids"), taxa referable to Ungulata (at least the earlier occurring taxa) have the following synapomorphies that also are seen (presumably convergently) in earliest primatomorphs (i.e., *Purgatorius*) and some later (but not earliest) anagalidans (e.g., the early rodent *Tribosphenomys*): molar conules with little or no internal wings; parastylar region reduced and with one cusp (a reversal, also found in the "zhelestid" *Alostera*); premolars four or fewer in number (although sirenians have five upper premolars, a reversal); parastylar groove (and lobe) reduced (also found in *Alostera*); metacingulum formed by postmetaconular crista continuing onto the metastylar region (also found in *Alostera*, but not earliest primatomorphs, i.e., *Purgatorius*). Differs from earliest primatomorphs (i.e., *Purgatorius*), some later (but not earliest) anagalidans (e.g., the early rodent *Tribosphenomys*), and from "Zhelestidae" in having upper molars rectangular in occlusal view, upper molar conules closer to protocone than to the midpoint of the tooth, mandibular condyle dorsal to the occlusal surface of the tooth row.

Discussion.—Some other autapomorphies suggested for Ungulata by Prothero (1993) are: more bunodont, lower-crowned teeth; molar trigonids anteroposteriorly shortened; M_3 with a large, posteriorly projecting hypoconulid; and astragalus with a shorter, robust head. Of these character states, the first two are found in all ungulatomorphs, the second is hinted at on the M_3 tentatively referred to *Eoungulatum kudukensis* (Fig. 13), and the fourth was not evaluated by us. Prothero (1993) also listed additional autapomorphies known with confidence only in living ungulates.

Many of the above-listed apomorphies of Ungulata are subsequently transformed or reversed within the tremendous taxonomic and ecologic radiation of ungulates. Thus, we feel that comparisons are justifiably limited to earliest Tertiary ungulates. We examined casts or specimens of most earliest Paleocene North America ungulates and found that the above character states are consistently present with the exception of some upper molars of *Mimatuta*

minuial. In PU 14211, cast of *M. minuial* figured by Van Valen (1978:pl. 7, fig. 4), the M^2 does not have a strong metacingulum formed by the postmetaconular crista continuing onto the metastylar region. Rather, as in "zhelestids" there is a moderate metacingulum formed only by the postmetaconular crista, while the metacrista runs from the apex of the metacone to the metastyle. We regard this as the primitive condition. On M^1 and M^3, however, the derived condition is found, in which the metacingulum is formed by the postmetaconular crista continuing onto the metastylar region. On the same cast, distinct postparaconule and premetaconule cristae are present. These cristae are only weakly developed compared to the much more prominent (and we believe, more primitive) wing-like cristae found in the western Asian Cretaceous ungulatomorphs.

The last apomorphy in the above diagnosis is the position of the mandibular condyle. As discussed earlier, a dentary assigned to *Sorlestes budan* preserves the mandibular condyle and is tentatively identified as a "zhelestid." If this is correct, "zhe- lestids" retain the primitive condition of having the inferior margin of the condyle at or near the level of the alveoli. The well-preserved dentary of *Sorlestes kara* from Kazakstan described by Nessov (1993:pl. 1) possesses a mandibular condyle at or only slightly higher than that of *Sorlestes budan* (Fig. 17A, B). When this position of the condyle is compared to that in earliest Tertiary ungulates (Archibald, 1996b:fig.4C, D), it is clear that, even in the earliest known archaic ungulates such as *Protungulatum donnae*, the mandibular condyle has shifted dorsally to a level above the occlusal surface of the tooth row.

This shift to a more dorsally placed mandibular condyle is correlated with herbivory, in which there is an increased emphasis on the masseter and pterygoid musculature and a concomitant reduction in the importance of the temporalis musculature (Janis, 1995). This dorsal shift of the condyle also results in the development of a simultaneous rather than sequential occlusion of the teeth (as seen in many modern carnivores), although the masticatory process can be considerably more complex (Greaves, 1995).

PHYLOGENETIC ANALYSIS OF UNGULATOMORPHA

Ungulate monophyly has been open to question, but studies using fossil or living taxa, or both, and various anatomical and macromolecular approaches suggest that at least six orders of living ungulate eutherians may form a monophyletic grouping (Novacek, 1992; Prothero, 1993). These are Artiodactyla, Cetacea, Hyracoidea, Perissodactyla, Proboscidea, and Sirenia. Interrelationships among these orders are still debated (e.g., see various articles in Szalay et al., 1993). Various extinct groups of eutherians are assigned to Ungulata, in part based on their resemblances to extinct archaic ungulates ("condylarths") and in part based on their possession of characters that are thought to be typical of ungulates (e.g., reduction of lateral digits, elongation of limbs, dental modifications towards herbivory). None of these approaches has proven especially strong, although several recent studies have argued for similar higher-level relationships among supposed extinct as well as extant ungulates (Prothero et al., 1988; Prothero, 1993; Archibald, in press), including archaic ungulates.

The major problem of diagnosing Ungulata, at least on anatomical characters, is that there is a tremendous amount of variation among extinct and extant orders, arguably more so than among any other hypothesized superordinal grouping of mammals. Archaic ungulates retain so many characters primitive for eutherians and lack so many of the characters found in later ungulate orders that the monophyly of Ungulata, including archaic ungulates is difficult to test. This means that the defining characters of Ungulata are essentially the same as those uniting archaic ungulates relative to other contemporary eutherians. The discovery by the first author of new ungulatomorphs (the "zhelestids") from the Late Cretaceous of western Asia, and their recognition in the Late Cretaceous of North America (Nessov, 1993), helps to clarify characters seen in earliest Paleocene archaic ungulates in North America and permits a more testable hypothesis of ungulate monophyly.

Figure 24 is the result of a phylogenetic analysis of ungulatomorphs ("zhelestids" and Ungulata) for which the upper dentition is known. *Protungulatum donnae* is used as an exemplar for Ungulata. We believe that it shows the primitive character states for Ungulata for most if not all of the characters that we examined. As noted in the discussion of the analysis in Figure 24, *Oxyprimus ericksoni* may be somewhat more primitive for some character states
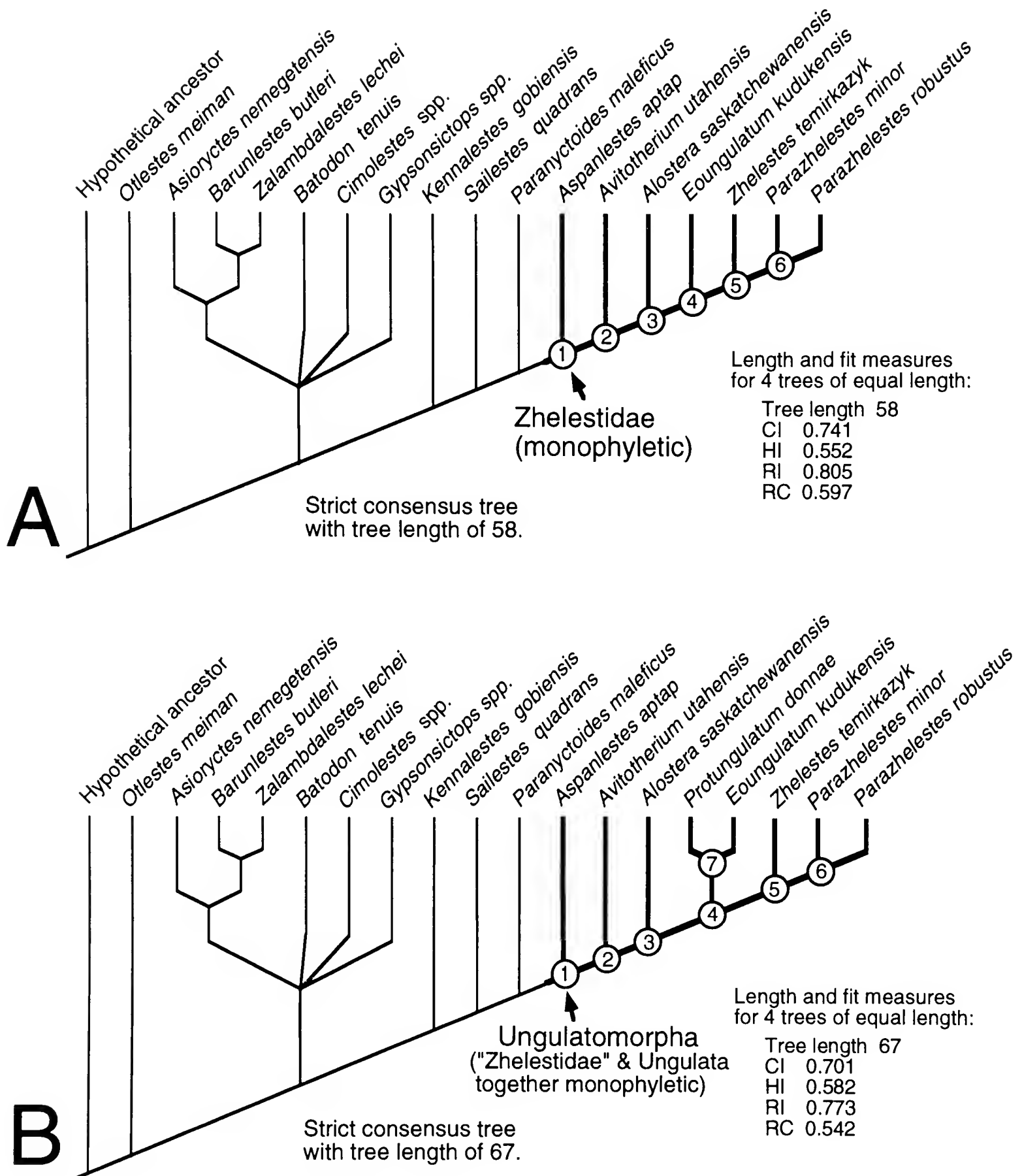
Fig. 24.—A. Strict consensus tree for all "zhelestids" and other Late Cretaceous mammals for which the upper dentition is reasonably known. B. Strict consensus tree for all taxa considered in A, plus the archaic ungulate *Protungulatum donnae*. Circled numbers in B refer to nodes discussed in text. In both analyses all taxa except the hypothetical ancestor were treated as a single polytomy. Tree length, consistency index (CI), homoplasy index (HI), retention index (RI), and rescaled consistency index (RC) shown in the lower right part of A and B are taken from the PAUP analysis for the number of trees (as indicated) with equal length. Tree lengths in the lower middle parts of A and B are from MacClade. In some cases (but not this one), tree lengths vary from PAUP to MacClade because PAUP treats polytomies as hard or as real polytomous speciations, while MacClade treats polytomies as uncertainties.

than is *Protungulatum donnae* (Luo, 1991), but choosing either of these taxa in the analysis does not affect the outcome.

Although the lower dentition was also examined, problems in differentiating taxa using lower dentitions and in assigning upper and lower dentitions to the same species precluded the effective use of lower dentitions in this analysis. Lower dental charac-

Table 3.—*Characters and character states of the upper dentition in a hypothetical ancestor, Late Cretaceous eutherians, the primato-morph* Purgatorius, *the rodent* Tribosphenomys, *and ungulatomorphs ("zhelestids" plus Ungulata, represented by* Protungulatum don-nae). *Primitive or ancestral state = 0. derived states = 1–3. See Figures 20–23.*

1) Degree of anteroposterior expansion of protocone: none (0); slight (1); moderate (2); substantial (3).

2) Degree of labial shift of protocone: none (0); moderate (1); substantial (2).

3) Postparaconular and premetaconular cristae: strong and wing-like (0); weak or absent (1).

4) Metacingulum: formed only by the postmetaconule crista and terminates dorsal to postmetacrista, which is continuous with the metastylar lobe (0); formed by the postmetaconule crista continuing onto the metastylar lobe (1).

5) Stylar shelf: wide (0); narrow (1).

6) Number of cuspules in parastylar region: one (0); two (1).

7) Pre- and postcingula: absent or poorly developed (0); present but do not reach or extend below the conules (1); present and reach or extend below the conules (2).

8) Height and size of paracone and metacone: paracone higher and larger (0); cusps of similar height and size (1).

9) Metacone or metaconal swelling on P^5 (or ultimate upper premolar): absent (0); present (1).

10) Number of premolars: five (0); four or fewer (1).

11) Shape of molar crown in occlusal view: triangular (0); trapezoidal (1); subrectangular (2); rectangular (3).

12) Constriction of crown through conular region with or without cingula present: no constriction, no cingula (0); marked constriction with cingula (1); slight constriction with cingula (2); no constriction with cingula (3).

13) Ectoflexus: deep (0); shallow (1); none (2).

14) M^3 linguolabial width relative to other molars: not markedly narrowed (0); markedly narrowed (1).

15) Parastylar groove: well developed (0); very reduced or absent (1).

16) Base of paracone and metacone: merged (0); separate (1).

17) Distance between paracone or metacone and protocone relative to total anterior or posterior width, respectively: between 45–55% of crown width (0); more than 55% of crown width (1); less than 45% of crown width (2).

18) Position of conules (especially paraconule) relative to paracone and metacone versus protocone: conules closer to midposition (0); conules closer to protocone than to the midposition (1).

ters are noted when they might provide further information about relationships. Characters and character states are described in Table 3; a taxon–character matrix is provided in Table 4.

In the two analyses shown in Figure 24, we chose to use as outgroups all demonstrably Late Cretaceous eutherians for which enough of the upper dentition is known to allow the coding of most of the 18 characters. One taxon not included in this analysis is *Kulbeckia* (Nessov, 1993), because at the time that the phylogenetic analysis was performed, specimens were not available for comparisons. For the two analyses in Figure 25, which we discuss at the end of this section, we also added the upper dentitions of the earliest known primatomorph, *Purgatorius unio*, and one of the better known early rodents, *Tribosphenomys minutus*. *Purgatorius unio* and *Tribosphenomys minutus* were included in this second set of analyses because their orders often have been placed in the grandorders Archonta and Anagalida respectively, which in turn have been linked to the grandorder Ungulata (McKenna, 1992; MacPhee and Novacek, 1993; Salles, 1995). These two species were chosen only as exemplars. They cannot be assumed to be primitive for all characters for their order or grandorder. Some of these issues are further discussed in the review of the analysis that follows.

We feel confident in assigning the primitive states for the 18 characters in the most recent common ancestor of all the taxa used in the analysis. This is based on the very wide distribution of these presumed primitive character states in Early Cretaceous eutherians, metatherian–eutherian grade mammals, and marsupials, as well as the outgroup taxa used in the analysis. These primitive states were assigned to the hypothetical ancestor given in Table 4 and shown in Figure 24. This was done in order to assess polarity for as many of the characters as possible that were used in the analysis. We could have also used the two-step analysis of Maddison et al. (1984) to help assess polarity of characters. The problem, however, is in choosing which of the 12 outgroups in Table 4 we believe is the sister taxon to ungulatomorphs. The arguments for such a choice are difficult to defend. We feel that running all outgroup and ingroup taxa as a single polytomy (unrooted tree) with one hypothetical ancestor was the more conservative and more justifiable approach given the present limited state of our knowledge. Further, using this approach, we feel justified in concluding that results are more robust because we have not limited potential sister-taxon relationships and we have not assumed monophyly of the ungulatomorphs. This is similar if not identical to the one-step method of Maddison et al. (1984).

Table 4.—*Character matrix for characters and states described in Table 3. Queried states (0?) were run using the state shown. Multistate characters were run as unordered. When more than one state occurs in a given taxon (0, 1), the state was run as polymorphic.*

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Hypothetical ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Outgroups (all Late Cretaceous eutherians represented by upper teeth)																		
Asioryctes nemegetensis	0	0	1**	0	0	0	0	0	?	1	0	0	0	0	0	0	0	0
Batodon tenuis	0	0	0	0	0	0	1	0	0	1	0	1	1	?	0	0	0	0
Barunlestes butleri	0	0	1	0	1?	0?	0	0	0	1[a]	0	0	0,1	?	0	0	0	0
Cimolestes spp.	0	0	0	0	0	0	0,1	0?	0	1	0	0,1	0,1	1	0	0	0	0
Gypsonictops spp.	0	0	0	0	1	0	1	0?	1	1	0	1	0,1	0	0	0	0	0
Keenalestes gobiensis	0	0	0	0	0	1	1	0	0,1	0,1	0	1,2	0	0	0	0	0	0
Paranyctoides maleficus	1,2	0	0	0	0	0	1	1	0	?	1	1,2	0	0	1	0	0	0
Otlestes meinan	0	0	0	0	0	0?	0	0	?	0	0	0	0	0?	0	1	0	0
Sailestes quadrans	1	0	0	0	0	1	1	0?	?	?	0	2	1	?	0	1	1	0
Zalambdalestes lechei	0	0	1?	0	0,1	0	0	0	1?	1	0	0	0	1	0	1	0	0
Outgroups (possible other zhelestid relatives with modern descendants, including ungulates)																		
Purgatorius unio	1	0	1**	0	1	0	2	1	1	1	3[c]	1	1	0?	1	1	0	0
Tribosphenomys minutus	1	1	1	1	1	0	2	1	?[d]	1?	1	3	2	0?	1	1	2	0
Protungulatum donnae	3	2	1	1	1	0	2	1	0,1	1[b]	3	3	1,2	0	1	1	2	1
Ingroup (presumptive zhelestids)																		
Alostera saskatchewanensis	1	0	0	1	1	0	2	1	?	?	1	2	2	?	1	1	1	0
Avitotherium utahensis	1	0	0	0	0	1	1,2	1	?	?	1	2	0,1	?	0	0	1	0
Aspanlestes aptap	1	0	0	0	0	1	2	1	1	0?	1	2	0,1	0	0	1	0	0
Zhelestes temirkazyk	1	0?	0	0	1	1	2?	1?	1	0	1	3	1	0	0	1?	2?	0
Parazhelestes robustus	2	1	0	0	1	1	2	1	0?	0?	1	3	1	1	0	1	2	0[e]
Parazhelestes minor	1,2	1	0	0	1	1	2	1	0,1	0?	1	2	1	?	0	1	2	0
Eoungulatum kudukensis	3	2	0	0	1	1	2	1?	1?	?	2	3	2	?	0	1	2	0

* Data for "outgroups" was obtained from casts, specimens, and the following sources: Lillegraven (1969), Kielan-Jaworowska (1975, 1981), Kielan-Jaworowska et al. (1979), Fox (1984, 1989), Cifelli (1990), Nessov et al. (1994), and Meng et al. (1994).

** Metaconule reduced.

[a] Premolars reduced to three.

[b] Although *P. donnae* is derived in having only four premolars, some ungulates such as sirenians have five upper premolars.

[c] The shape is actually more hourglass than rectangular because the hypoconal region is appended to the posterior part of the molar rather than forming a more integrated part of the crown as in most Ungulata. Thus, homology of the character in these two taxa is doubtful.

[d] The ultimate premolars described and figured by Meng et al. (1995) appear to be deciduous, and thus the condition of the permanent ultimate premolars remains unknown (Wyss, personal communication).

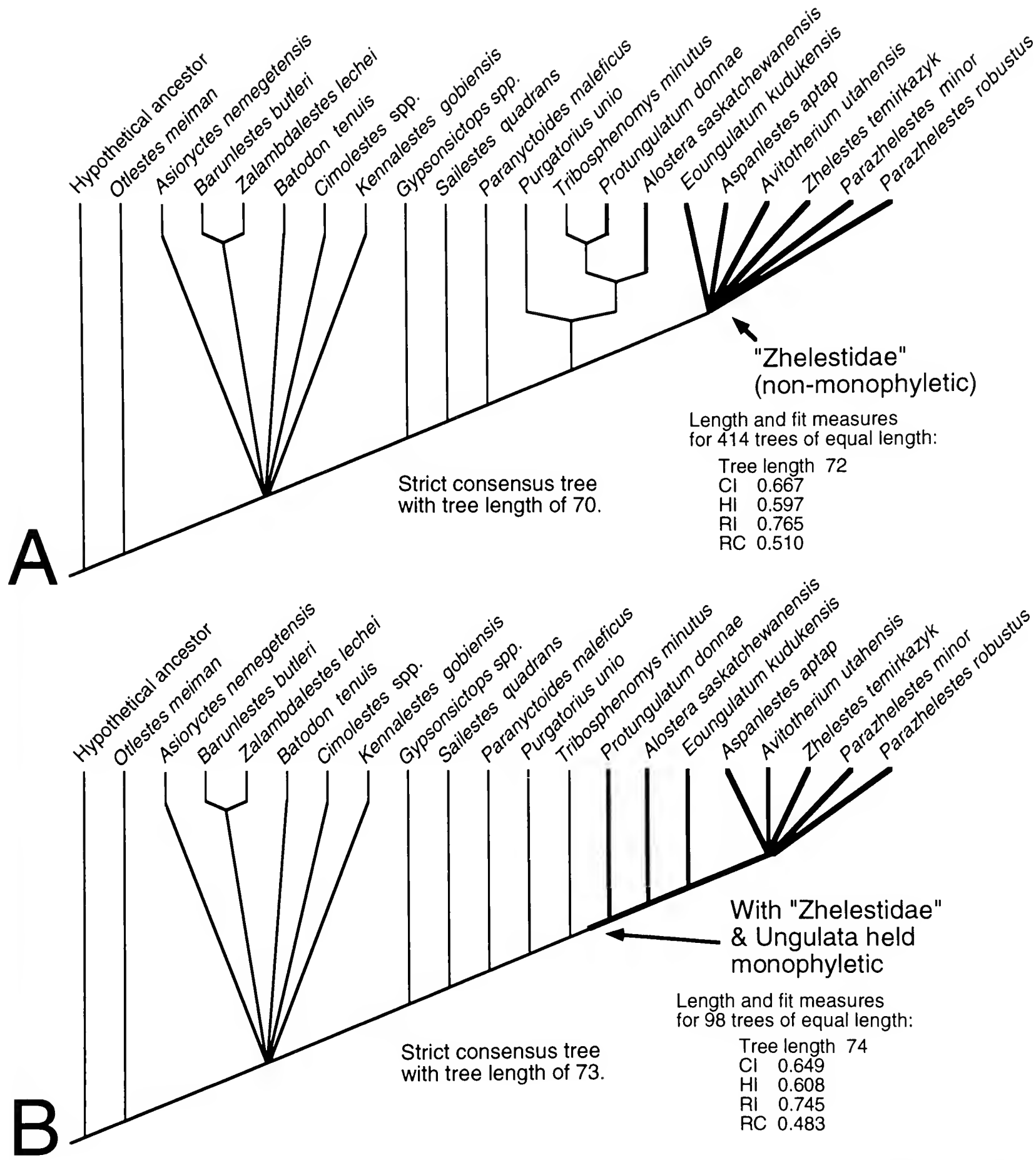[e] Character state was incorrectly coded as "1" in Archibald (1996b).

Fig. 25.—Strict consensus trees for all "zhelestids" and other Late Cretaceous mammals for which the upper dentition is reasonably known, plus *Protungulatum donnae* (an archaic ungulate), *Purgatorius unio* (an early primtomorph), and *Tribosphenomys minutus* (an early rodent). In the analysis in A all taxa, except the hypothetical ancestor, were treated as a single polytomy. In the analysis in B, "zhelestids" plus *P. donnae* were constrained to be monophyletic, while all other taxa, except the hypothetical ancestor, were treated as a single polytomy. Tree length, consistency index (CI), homoplasy index (HI), retention index (RI), and rescaled consistency index (RC) shown at lower right are taken from the PAUP analysis for the number of trees with equal length as indicated. The alternative tree lengths shown at lower middle are from MacClade. In some cases, tree lengths vary from PAUP to MacClade because PAUP treats polytomies as "hard" or as real polytomous speciations, while MacClade treats polytomies as "soft" or as uncertainties, hence the lower tree lengths for MacClade.

The taxon–character matrix in Table 4 was created on MacClade 3.01 (Maddison and Maddison, 1992) and analyzed using PAUP 3.1.1 (Swofford, 1993). All multistate characters were treated as unordered in all analyses. Opinions vary on the efficacy of ordering, from those arguing against it (Hauser and Presch, 1991) to those arguing for it in some cases (Campbell and Frost, 1993). Although we do not have a strong opinion, we do feel that when well demarcated, biologically defensible transitions can be discerned that ordering is a reasonable approach. In the case of the present study, however, changes between taxa are generally small, forming a graded series. Thus, without more clearly demarcated changes, ordering seems unjustified for our study.

For the two analyses in Figure 24, we employed the branch-and-bound algorithm in PAUP and, as noted, ran the analysis starting with the hypothetical ancestor as the single outgroup, with all the remaining outgroup taxa and the ingroup taxa as a single polytomy. For the two analyses in Figure 25, we employed the heuristic search algorithm in PAUP. For the analysis in Figure 25A we started with all the outgroup and ingroup taxa as a single polytomy and the hypothetical ancestor as the single outgroup. For Figure 25B we started with all ungulatomorph taxa ("zhelestids" plus *Protungulatum donnae*) as a polytomy that was, in turn, monophyletic relative to the outgroup taxa. The outgroup taxa were run as a single polytomy and the hypothetical ancestor as the single outgroup.

The number of equally parsimonious trees, tree lengths, and measures (consistency index, homoplasy index, retention index, and rescaled consistency index) from each PAUP run are given in Figures 24 and 25. For the strict consensus trees we employed the "soft polytomy" option in MacClade, which assumes uncertainty at these polytomies, rather than the "hard polytomy" option in PAUP, which assumes multiple speciations. Thus, the tree lengths for the strict consensus trees generated from MacClade (shown in Fig. 25) are slightly lower than the tree lengths for the comparable PAUP run.

In the following discussion, characters and their states are identified by the same numbering system used in Tables 3 and 4. For example, the derived state of the stylar shelf (5) is narrow (1), and is referred to as [5.1], while the primitive wide shelf is [5.0]. Relevant nodes in Figures 24A and B are numbered and circled. These are the nodes to which we refer in the following discussion. The character state changes are the same at the similarly num-

bered nodes in Figures 24A and B unless indicated otherwise. As each node is discussed, it is noted whether an apomorphy is shared only at that node (unambiguous) or occurs among other taxa (see Table 4) in the analysis (ambiguous). Possible autapomorphies for each terminal taxon are also noted. Only those nodes and terminal taxa that directly include "zhelestids" and/or *Protungulatum donnae* are considered in the following discussion.

As noted earlier, there are no synapomorphies that unite "zhelestids" as a monophyletic taxon whenever ungulates such as *Protungulatum donnae* (Fig. 24B) are included in the analysis, but for convenience we use the term for this paraphyletic assemblage (with quotation marks). Some character states, such as the twinning of cusps on the talonid, appression of trigonid cusps, reduction of M^3 and M_3, and closeness of conules to paracone and metacone were first thought to be possible synapomorphies of the Asian "zhelestid" taxa. On further analysis, which is detailed below, some of these character states, such as reduction of M^3 and M_3, appear to be derived for only some species of "zhelestids." Other character states are more easily explained as transitions to later taxa, for example, twinning of cusps on the talonid and appression of trigonid cusps appear related to the expansion of the talonid and the "squaring" of the molar seen in later archaic ungulates.

Node 1 in Figure 24A unites the clade Zhelestidae as a monophyletic taxon, while in Figure 24B "Zhelestidae" is not monophyletic with the inclusion of *Protungulatum donnae* (an ungulate). However, a more inclusive clade containing "Zhelestidae" and *P. donnae* remains monophyletic in Figure 25B, and this assemblage ("zhelestids" + ungulates) was earlier named Ungulatomorpha (Archibald, 1996*b*). Ungulatomorpha in Figure 24B (and Zhelestidae in Figure 24A) share the following three apomorphies: stylar shelf narrow [5.1], pre- and postcingula reach or extend below conules [7.2], and metacone or metaconal swelling on ultimate upper premolar [9.1]. Among Late Cretaceous eutherians, narrowing of the stylar shelf [5.1] occurred at least two times (*Barunlestes* + *Zalambdalestes* and *Gypsonictops*) and a metacone or metaconal swelling [9.1] arose up to three other times (possibly *Kennalestes*, *Gypsonictops*, and *Zalambdalestes*).

In addition to these apomorphies of the upper dentition, the lower dentition (where known) of ungulatomorphs has four apomorphies and one possible apomorphy that were not included in the phy-

logenetic analysis. We regard the expansion of the talonid, twinning of the entoconid and hypoconulid, lowering of the trigonid height relative to the talonid, and slight appression (or anteroposterior shortening) of the trigonid cusps as ungulatomorph apomorphies. The expansion of the talonid is unarguably related to the expansion of the protocone in the upper molars. Luo (1991) noted, however, that the talonid on the M_1 of at least some early Tertiary ungulates such as *Protungulatum, Oxyprimus,* and *Mimatuta* is actually the smallest relative to the size of the trigonid as compared to at least four other Late Cretaceous and early Tertiary eutherians (*Cimolestes, Procerberus, Gypsonictops,* and *Purgatorius*). How widespread this relative size pattern for the talonid is, and whether it is primitive or derived for these early Tertiary ungulates, remains to be studied. The twinning of the entoconid and hypoconulid could be an autapomorphy that would argue for the monophyly of "Zhelestidae." It seems more likely that this twinning is also a result of the expansion of the protocone, caused as the hypoconid moved away from the other two talonid cusps, similar to the twinning that occurred in marsupials (Marshall and Kielan-Jaworowska, 1992). By the time the ungulate grade is reached, further expansion of the talonid basin has forced the entoconid and hypoconulid apart. Nessov (personal observation) felt, however, that he could detect some twinning of the entoconid and hypoconulid on some specimens of early Tertiary ungulates such as the M_2s of species of *Mimatuta* and *Ragnarok* (see various figures in Archibald, 1982; Lofgren, 1995). Appression of the trigonid cusps and lowering of the trigonid relative to the talonid are related to the early stages of the "squaring" of molars leading to herbivory. As with the metacone on the P^5 [9.1], the metaconid on P_5 probably evolved convergently in other Late Cretaceous eutherians.

At node 2, (Fig. 24A, B) all ungulatomorphs except *Aspanlestes* can be distinguished by the apomorphy of having the distance between the paracone or metacone and protocone relative to the anterior or posterior width, respectively, either more than 55% of the crown width [17.1] or less than 45% of the crown width [17.2]. *Aspanlestes* retains the primitive state [17.0] of having the distance between paracone or metacone and protocone relative to anterior or posterior width, respectively, at between 45% and 55%. This is the state found in all other Late Cretaceous eutherians examined except *Sailestes,* which exhibits the derived state [17.1]. This appears to be convergent with the "zhelestids"

Avitotherium and *Alostera* that also have state 17.1, because the relatively greater distance between paracone and metacone and protocone in *Sailestes* is a result of the transverse narrowing of the entire crown.

At node 3, (Fig. 24A, B) all ungulatomorphs except *Aspanlestes* and *Avitotherium* can be distinguished by the apomorphy of having the ectoflexus either shallow [13.1] or absent [13.2]. Depth of the ectoflexus is a rather homoplastic character, having become at least somewhat shallow in a wide variety of other Late Cretaceous eutherians (*Barunlestes, Batodon, Cimolestes, Gypsonictops,* and *Sailestes*). Even in *Aspanlestes* and *Avitotherium,* there is some suggestion of shallowing.

Neither *Aspanlestes* nor *Avitotherium* possess any autapomorphies in either the upper or lower dentition that convincingly argue for their respective monophyly. Their character states are primitive retentions of other Late Cretaceous eutherians or all ungulatomorphs. These species are, however, distinctly smaller than all other "zhelestids," which is a questionable autapomorphy for these species.

At node 4, (Fig. 24A, B) all ungulatomorphs except *Aspanlestes, Avitotherium,* and *Alostera* possess the following two apomorphies: the crown is not constricted through the conular region and cingula are present [12.3] (except in *Parazhelestes minor,* which shows a presumed reversal to a slight constriction, but cingula are present [12.2]); and the distance between the paracone or metacone and protocone relative to the anterior or posterior width, respectively, is less than 45% of the crown width [17.2].

Alostera saskatchewanensis shows three autapomorphies that are convergent on ungulates such as *Protungulatum donnae.* These are: metacingulum formed by the postmetaconule crista continuing onto the metastylar lobe [4.1], number of cuspules on parastylar region is one [6.0], and parastylar groove absent [15.1]. If the lowers of *Alostera saskatchewanensis* are properly referred to this species (Fox, 1989; Storer, 1991), the probable loss of twinning of the entoconid and hypoconulid is another autapomorphy. This combination of character states suggests that *Alostera* could simply be an odd archaic ungulate, but the parsimony argument of our analysis suggests otherwise.

At node 5, (Fig. 24A, B) *Zhelestes, Parazhelestes robustus,* and *Parazhelestes minor* are united by the rather weak character of possessing a shallow ectoflexus [13.1], presumably reversed from having none [13.2]. An equally likely possibility is that the

ectoflexus became shallow [13.1] at node 4 (Fig. 24A, B) and then disappeared at least twice [13.2], once leading to *Alostera* and again on the stem leading to the *Eoungulatum* + Ungulata clade.

Zhelestes temirkazyk does not possess any clear autapomorphies arguing for its monophyly. Further, it is based on a single, heavily worn maxillary dentition. Assuming that it is a taxon separate from other "zhelestids," a possible autapomorphy is the relatively anteroposteriorly narrow crowns of M^{1-2}. This can be seen in a comparison of "zhelestid" upper molars in Figure 20, as well as the offset placement of this species in the graph of lengths versus widths in Figure 6. Only the M^2 of *Parazhelestes minor* shows a similar placement on these graphs (Fig. 6).

At node 6 (Fig. 24A, B), *Parazhelestes robustus* and *P. minor* are united by the following apomorphies: amount of anteroposterior expansion is slight to moderate [1.1/2] or moderate [1.2], amount of labial shift of the protocone is moderate [2.1]. These are rather weak potential synapomorphies, being minor intermediate states possibly within an evolutionary gradient. A potentially much better apomorphy uniting these two species is the linguolabial narrowness of M^3 [14.1]. Unfortunately, M^3 is unknown in *P. minor* and this character was therefore coded as missing [14.?] for this species.

Parazhelestes minor does not possess any clear autapomorphies. Its smaller size compared to *P. robustus* could be derived or ancestral. The relative anteroposterior narrowing of the crown of M^2, similar to the condition seen in *Zhelestes temirkazyk*, could be an autapomorphy. We retain *P. minor* as monophyletic, but realize that it could also be a metaspecies (i.e., a previously named portion of a polytomy for which positive evidence of monophyly or paraphyly is lacking, in this case at the species level where the included organisms lack any synapomorphies that would unite them; Archibald, 1994). In *Parazhelestes robustus*, the M^3 is distinctly narrowed lingually [14.1] (Fig. 11, 20). Because we do not have information on the size of M^3 in *P. minor*, we do not know whether the reduction of M^3 is characteristic of both species of *Parazhelestes*. For now, we treat this as a possible autapomorphy for *P. robustus*. We also do not know whether reduction of M^3 is shared with any other species of "zhelestid," although it is known that M^3 is not linguolabially narrowed [14.0] (Fig. 9, 20) in *Zhelestes temirkazyk* and *Aspanlestes aptap*. Some reduction of M^3 and M_3 may be characteristic of some or all "zhelestids," and, of course, occurs in other ungu-

late clades as well. The M_3 in *Kumsuperus avus* is similar in width to M_3 in the smaller *Aspanlestes aptap*, but is substantially narrower compared to that in the similarly sized *Sorlestes budan*. In *Eoungulatum kudukensis*, if M_3 is correctly associated with M_2 (both teeth are tentatively assigned), M_3 appears to be unreduced in this species. The possible importance of M^3 and M_3 reduction in "zhelestids" awaits the recovery of additional specimens.

In Figure 24A *Eoungulatum kudukensis* has the following three autapomorphies: amount of anteroposterior expansion of the protocone is substantial [1.3], amount of labial shift of the protocone is substantial [2.2], and shape of the molar crown is subrectangular [11.2].

At node 7 in Figure 24B, when Ungulata (as represented by *Protungulatum donnae*) is added to the analysis, all three of these character states unite *E. kudukensis* and Ungulata (as represented by *P. donnae*). The shape of the molar crown is further modified in *P. donnae* by becoming rectangular [11.3].

Finally, the phylogenetic analysis in Figure 24B argues strongly for the monophyly of (grandorder) Ungulata (as represented here by *Protungulatum donnae*). The following seven states are interpreted as derived relative to all other members of Ungulatomorpha (i.e., "Zhelestidae"): molar conules with little or no internal wings [3.1]; metacingulum formed by postmetaconular crista continuing onto the metastylar region [4.1]; parastylar region reduced with one cusp [6.0 reversal]; premolars four or fewer in number [10.1], although sirenians have five upper premolars (Gingerich et al., 1994), which we regard as a reversal; upper molars rectangular in occlusal view [11.3]; parastylar groove (and lobe) reduced [15.1]; and conules closer to the protocone than to the midposition of the crown [18.1]. Of these, only two, [11.3] and [18.1], are unique to Ungulata as compared to the other taxa used in this analysis.

For the analyses shown in Figures 25A and B we added the earliest known primatomorph *Purgatorius unio* and the early rodent *Tribosphenomys minutus*. The overall pattern was similar to that in Figure 25A, other than the addition of these two taxa, described above (Fig. 24A, B). In Figure 25B the one difference was that the analysis started by holding all ungulatomorph taxa as a monophyletic polytomy.

Unsurprisingly, in the analysis shown in Figure 25A, Ungulatomorpha was rendered nonmonophyletic. *Purgatorius, Tribosphenomys, Protun-*

gulatum, and *Alostera* were united by three character states: conular wings weak or absent [3.1], reduction of premolars from five to four or fewer [10.1], and parastylar groove (and parastylar lobe) reduced or absent [15.1]. The possible clustering of the grandorders Archonta (including *Purgatorius*), Anagalida (including *Tribosphenomys*), and Ungulata (including *Protungulatum* and *Alostera*) is suggested by various authors (McKenna, 1992; MacPhee and Novacek, 1993; Salles, 1995). Of the three character states uniting the above taxa, the first and second are also found in a variety of other Late Cretaceous eutherians. These include *Zalambdalestes* and *Barunlestes*, which are sometimes placed together with a variety of other eutherians, including rodents, within Anagalida (Stucky and McKenna, 1993). If this alignment is true, the above character states are convergent in at least rodents and ungulates.

There is nothing that we currently know about the dentition of "zhelestids" that would preclude them from giving rise to rodents such as *Tribosphenomys minutus*. There is, however, nothing that especially links "zhelestids" and anagalidans, the more inclusive taxon to which rodents such as *T. minutus* may belong. Further, some of the outgroup taxa such as *Zalambdalestes* and *Barunlestes* that have either been implicated in anagalidan ancestry or sometimes even included in Anagalida (Stucky and McKenna, 1993; but see Kielan-Jaworowska, 1978, for arguments against anagalidan affinities of Zalambdalestidae) retain a number of primitive eu-

therian upper dental features (as well as showing specializations) not found in "zhelestids." For example, these two genera retain the primitive states in characters 1, 7, 11–13, and 17 that are derived in "zhelestids" (see Table 4). The retention of these primitive dental features in alleged anagalidans but not in ungulatomorphs suggests that most if not all of the apomorphic dental similarities of "ungulatomorphs" and *T. minutus* are convergent adaptations for herbivory.

As to a primatomorph–ungulatomorph connection, some of the upper dentitions of "zhelestids" such as *Aspanlestes* and *Avitotherium* (which retain more primitive character states) suggest possible primate as well as ungulate ancestry. When the lower dentitions (especially of the better-known *Aspanlestes*) are examined, however, a possible primatomorph–ungulatomorph link seems less likely. In "zhelestids" the molar trigonids already have greater anteroposterior shortening than that seen in early primatomorphs. Thus ancestry of primatomorphs, although possibly near that of "zhelestids," would probably be outside this taxon.

In Figure 25B, in which Ungulatomorpha was constrained to be monophyletic, *Purgatorius* and *Tribosphenomys*, unsurprisingly, form the second and first outgroups, respectively, to Ungulatomorpha. This possible primatomorph–rodent (or anagalidan)–ungulatomorph relationship is intriguing. However, until we have more definitive data, we prefer to err in the more conservative direction in excluding rodents and primatomorphs from Ungulatomorpha.

BIOGEOGRAPHIC AND PALEOECOLOGICAL CONSIDERATIONS

As discussed in the Introduction, there is some issue as to the age of the earliest archaic ungulates in North America. Archaic ungulate-bearing sites in the Frenchman Formation, Saskatchewan, Canada (Fox, 1995), appear to be latest Cretaceous (Lancian) in age, while those to the south in eastern Montana, U.S.A., appear to be earliest Paleocene (Puercan) in age. Ungulatomorphs, however, are clearly present (barring rampant convergence) in North America in the form of the "zhelestid" *Avitotherium* by the middle Campanian (Judithian) at sites in south-central Utah (Cifelli, 1990) and north-central Montana (Montellano, 1992:fig. 29; upper molar identified by her as cf. *Paranyctoides*), both U.S.A.; and linger as the "zhelestid" *Alostera* in latest Cretaceous (Lancian) and

earliest Paleocene (Puercan) sites in eastern Montana, U.S.A., and southern Saskatchewan and Alberta, Canada.

As is clear from our alpha-level taxonomy of "zhelestids," their known center of greatest and oldest diversity is in western Asia. It thus may seem surprising that ungulatomorphs, both as "zhelestids" and archaic ungulates, are found in the Late Cretaceous and early Paleocene of North America, and even the early Paleocene of South America, but are unknown from comparably aged faunas in China and Mongolia. The absence of early Paleocene ungulatomorphs from central and eastern Asia may well be the result of the absence of sites of the appropriate age there. However, this is not the case for the Late Cretaceous of central Asia, for which very

rich Late (but not latest) Cretaceous mammal sites are known. Ungulatomorphs are most likely absent from Late Cretaceous faunas in central and eastern Asia for paleoecological reasons.

In the Gobi Desert of central Asia, the Upper Cretaceous Djadokhta and Barun Goyot formations (Kielan-Jaworowska, 1984) were deposited in more inland areas with semi-arid and arid climates (Verzilin, 1978; Jerzykiewicz, 1989; Jerzykiewicz and Russell, 1991). In sharp contrast, most of the Upper Cretaceous formations in North America that have produced extensive vertebrate faunas were formed on low coastal plains (Archibald, 1996a) that were seasonally dry but certainly not arid (Fastovsky and McSweeny, 1987). This is especially well demonstrated by similarities in the Late Cretaceous non-mammalian vertebrate faunas of western North America (Estes, 1964; Estes et al., 1969; Estes and Berberian, 1970; Bryant, 1989) and western Asia (Nessov, 1992; Nessov et al., 1994), compared to central Asia. The former two regions have a number of elements in common, including sharks, bony fishes, amphibians, turtles, and crocodilians. These faunal elements are far less common or absent at the central Asian sites.

We are hard pressed to draw similarly strong paleoecological inferences using Late Cretaceous mammals. This is in part because of the poor quality of preservation for North American forms; more importantly, the mammal material usually does not permit us to draw similarly strong ecological conclusions by analogy with modern mammals as is possible for many nonmammalian fossil vertebrates (e.g., fishes and amphibians). Nevertheless, the profound differences among the Late Cretaceous mammal faunas of western Asia, central Asia, and western North America may well have been ecologically driven. This may explain the absence of ungulatomorphs from the more arid central Asian sites, while they are the most common mammalian taxa in the more lowland western Asian sites and even have a small presence in the lowland sites of western North America.

In sharp contrast to the above pattern, multituberculates are a very common taxonomic component in Late Cretaceous faunas of both central Asia and western North America, while they are very rare in western Asia. In numbers of collected specimens, they comprise on average about 70% in central Asia (Kielan-Jaworowska, 1992) but only 1% in western Asia (Kielan-Jaworowska and Nessov, 1992). Comparable estimates are not available for the Late Cretaceous of western North America, but multituber-

culates undoubtedly comprise 50% or more of the mammal specimens. Multituberculates are predominantly or totally taeniolabidoids in central Asia while in western North America they are predominantly ptilodontoids. Thus, the similarity in the multituberculate faunas between these two areas is more illusory than real. It is only near the Cretaceous/Tertiary boundary that taeniolabidoids become an important component of the mammal fauna in North America, presumably via invasion through Beringia from central Asia (e.g., Lillegraven et al., 1979). Lacking earliest Paleocene sites in central Asia, we cannot say whether the opposite pattern of migration into central Asia was also true for ptilodontoids.

The extremely low presence of multituberculates in western Asia seems anomalous. The only named multituberculate from western Asia is *Uzbekbaatar kizylkumensis*, which cannot be confidently identified as taeniolabidoid or ptilodontoid (Kielan-Jaworowska and Nessov, 1992). If one hypothesizes that "zhelestids" and multituberculates were ecological competitors, then the absence of the latter in western Asia might be explained. Based on dentitions, "zhelestids" may have filled an ecological role similar to the abundant marsupials in the Late Cretaceous of North America, yet there is a considerable diversity and abundance of multituberculates in the Late Cretaceous of North America.

Archaic ungulates appear in North America just before, at, or just after the Cretaceous/Tertiary boundary, which is similar to the pattern of taeniolabidoid appearance in North America. Unlike the taeniolabidoids, most of which can be confidently traced to central Asia, we are not certain from whence the archaic ungulates came. Ancestral archaic ungulates may have been evolving in situ in North America at least since the middle Campanian (Judithian) from "zhelestids" such as *Avitotherium*, but the relatively well-documented Late Cretaceous record of this continent shows no such trace except for the rather enigmatic *Alostera*. Archaic ungulates also might have come from Europe or even eastern North America near the close of the Cretaceous, arising from the questionable "zhelestids" known from those regions. A more appealing, but equally unsubstantiated hypothesis is that they came from western Asia along coastal routes over Beringia to North America (Nessov et al., 1994; Archibald, 1996a). This is appealing because of the considerable diversity of "zhelestids" in western Asia and because of the precocious presence of such advanced "zhe-

lestids" as *Eoungulatum* in western Asia, which is almost at the archaic ungulate grade of evolution. The most sobering aspect of this scenario is the tremendous amount of time separating the western Asian "zhelestids" and the earliest North American archaic ungulates, probably more than 20 million years from the Coniacian (~87 million years ago) to the Cretaceous/Tertiary boundary at ~65 million years. Much could and did transpire during this 20+ million year interval for which we have little fossil evidence at present.

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Note added in proof:

In 1997, L. B. Golovneva and A. O. Averianov edited a posthumously published monograph by L. A. Nessov in which the unpublished names *Parazhelestes minor* (pp. 148 and 213), *Eoungulatum* (p. 150), and *Eoungulatum kudukensis* (p. 213) were used without being "accompanied by a description or definition that states in words characters that are purported to differentiate that taxon. . ." (Article 13[a][i] of the International Code of Zoological Nomenclature, Third Edition, 1985). Accordingly, the aforementioned taxonomic names are nomina nuda in Nessov, 1997. When used in the article by Nessov (1997), these nomina nuda were accompanied by the citations Nessov et al. or Nessov et al., in press, in reference to the publication here presented, but without this citation in the references of Nessov, 1997. Thus, the correct attribution of these taxonomic names is the present work (Nessov, Archibald, and Kielan-Jaworowska, 1998). The complete citation for Nessov, 1997 is: Nyemorskiye pozvonochnýye myelovogo pyerioda Syevyernoi Yevrazii (Cretaceous nonmarine vertebrates of northern Eurasia). Sankt-Pyetyerburgskii Gosudarstvyennýi univyerityet Nauchko-isslyedovatyelskii institut zyemnoi korý (in Russian with English summary).

Two new genera and species were described and figured in Nessov (1997) as belonging to Zhelestidae. The first is *Eozhelestes mangit* based on a single, lower molar identified as a left M_1 from the Cenomanian-aged Sheikhdzheili locality (SSHD-8), western Uzbekistan. The second is *Ortalestes tostak* based on a single upper tooth identified as a left M^1 from the Coniacian-aged Dzharakuduk locality (CBI-4). These specimens were examined by the second author (JDA). Space does not permit a full discussion, but a few comments are in order. The type of *Eozhelestes mangit* does appear to be either M_1 or M_2. Although there is nothing precluding a mammal with this kind of lower molar and of this earlier age from being

ancestral to "zhelestids," it lacks the expanded talonid of "zhelestids" and later ungulatomorphs. Accordingly, it is excluded from Ungulatomorpha (including "Zhelestidae"). The upper tooth identified as a left M^1 from Dzharakuduk has been somewhat damaged since the time of being photographed. It is slightly smaller than M^1s but similar in size to P^5s of *Aspanlestes aptap,* also from Dzharakuduk. It has dental attrition, a lack of roots, and a somewhat linguolabially narrowed crown suggestive of a dP^5. Thus, it seems quite likely that the single and only known tooth of *Ortalestes tostak* is a dP^5 of *Aspanlestes aptap.*

CHINESE PALEOCENE MAMMAL FAUNAS AND THEIR CORRELATION

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ABSTRACT

Recent advances in knowledge of Chinese Paleocene mammal diversity, biostratigraphy, and the geochronology of mammal-bearing rock units in China are reviewed. In addition to 22 recently described species, systematic revision of a number of taxa has altered the composition and correlation of Chinese Paleocene mammal faunas. Based on these data, new intracontinental correlations are proposed for Paleocene mammal localities within China, and the intercontinental correlation of these Chinese Paleocene faunas with the established North American sequence of provincial land mammal ages is critically reevaluated. In contrast to earlier views, correlation of the boundary between the Shanghu and Nongshan formations (Nanxiong Basin, Guangdong Province) with that between the Shizikou and Chijiang formations (Chijiang Basin, Jiangxi Province) with the middle part of the Upper Member of the Wanghudun Formation (Qianshan Ba-

sin, Anhui Province) is proposed here. Moreover, some rock units and faunas that were previously thought to be early Eocene in age are considered here to be late Paleocene. Although most Chinese Paleocene mammals are endemic at the generic rank, certain taxa are closely related to North American forms, providing evidence for intercontinental biostratigraphic correlation between Asia and North America during the Paleocene. Based on this evidence, the Torrejonian/Tiffanian boundary appears to lie within the Nongshanian, while the Tiffanian/Clarkforkian boundary occurs within the Gashatan. The first radiometric date for the Chinese Paleocene, 61.63 ± 0.92 Ma (derived from a basalt sample from Xinzhou in Hubei Province), and the paleomagnetic records of the lower Paleocene in China are consistent with intercontinental correlation of the Torrejonian/Tiffanian boundary within the Nongshanian.

INTRODUCTION

Paleocene mammals were unknown in China prior to Chow's description of the dinoceratan *Prodinoceras turfanensis* from Xinjiang in 1960 (Chow, 1960). Since then, continuous work by Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) colleagues, frequently assisted by many people and organizations in a number of Chinese provinces and by colleagues from other institutions, has demonstrated the presence of Paleocene mammals in more than a dozen basins in China. These

include (Fig. 1): the Nanxiong and Sanshui basins in Guangdong; the Chijiang Basin in Jiangxi; the Chaling Basin in Hunan; the Qianshan, Xuancheng, Jiashan, and Tongling basins in Anhui; the Xinzhou Basin in Hubei; the Tantou Basin in Henan; the Shimen and Shanyang basins in Shaanxi; the Turfan (Turpan) Basin in Xinjiang; and the Erlian (Erenhot) Basin in Nei Mongol (Li and Ting, 1983; Russell and Zhai, 1987; Xue et al., 1987; Zhou et al., 1995; Huang and Chen, 1997; Wang and Zhang, 1997). The work of all these researchers resulted in numerous publications and the description of many species of Paleocene mammals, which document the

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[1] Minchen Chow died January 4, 1996, while this manuscript was under preparation.

most nearly complete record of Paleocene mammals known from Asia. On the basis of this work, the first Chinese Paleocene mammal-based biostratigraphic sequence was established (South China "Red Beds" Research Group, IVPP, 1977).

Paleocene continental strata in the basins cited above preserve an important mammalian record of early through late Paleocene age, a record that is important not only for purposes of biostratigraphic correlation but also for hypotheses on the phylogeny and biogeography of high-level mammal taxa (e.g., rodents, lagomorphs, perissodactyls, arctosty-lopids) at the beginning of the Cenozoic. In the 1980s, Li and Ting (1983) and Russell and Zhai (1987) reviewed the Paleocene mammal record of China in their synopses of Chinese and Asian Paleogene mammals and stratigraphy, respectively. Our goal here is to provide an update on recent advances regarding the Paleocene of China, which not only enrich the known Chinese Paleocene mammal faunas taxonomically, but also allow for more refined biostratigraphic correlations within China and between Asia and North America during the Paleocene.

GEOLOGICAL SETTING OF MAMMAL-BEARING PALEOCENE BASINS IN CHINA

From the late Mesozoic through the early Cenozoic, tectonic activity resulted in the development of a number of small intermontane basins in the eastern part of China and in some mountain ranges as well as a few larger basins in northern China. Some of these basins have been shown to possess Paleocene strata that yield the fossil remains of mammals living in these areas at that time. The following paragraphs provide a brief introduction to the geological and paleoenvironmental context, insofar as it is known, for interpreting the Paleocene mammal record of China.

1. NANXIONG BASIN, GUANGDONG (FIG. 1:1)

In the Nanxiong Basin, mammal-bearing Paleocene strata overlie the late Cretaceous Nanxiong Formation (= Nanxiong Group of Zhao et al., 1991) and are separated by an unconformity from the overlying Danxia Group (or Formation), which varies in age from late Paleocene to late Eocene. The Paleocene mammal-bearing rocks have been divided into the Shanghu Formation (= Shanghu Member of the Lofochai Formation of Zhou et al., 1977) and the overlying Nongshan Formation (= Nongshan Member of the Lofochai Formation) by Tong et al. (1976). The Shanghu Formation, with a thickness ranging from 470 to over 600 m, comprises purplish red mudstones, intercalated with thin sandstones and conglomerates, and sandy mudstones. The sporo-pollen record from the Shanghu Formation indicates a mixed forest vegetation of conifers, evergreen broad-leaf, and deciduous broad-leaf trees living under a warm temperate to subtropical climate (M. Li, 1989). The Nongshan Formation has a thickness ranging from 220 to 320 m and was further subdivided into the Zhuguikeng and Datang members (Tong et al., 1976). The lower Zhuguikeng Member consists of grayish green and purplish red mudstone intercalated with sandstone, while the upper Datang Member is composed of interbedded purplish red mudstone and siltstone with intercalating sandstone. The age of the Nongshan Formation has been variously interpreted as Eocene or early Eocene (e.g., Chen and Shen, 1979; He, 1979; Huang, 1979; Li, 1983; Chen, 1986), late Paleocene to early Eocene (Yang, 1979), or late Paleocene (Zhang, 1984) on the basis of invertebrate, plant, and pollen records. Because we believe the fossil mammals from the Nongshan Formation provide the best evidence for division and correlation, we follow mammal-based correlations of the Nongshan Formation here, which unanimously advocate the age of this unit to be middle or late Paleocene. Li (1983) proposed that the assemblage of pollen and spores from the Nongshan Formation (= Lofochai Formation; Li, 1983) represented a mixed forest of evergreen broad-leaf and deciduous broad-leaf vegetation in subtropical to tropical climatic conditions.

2. SANSHUI BASIN, GUANGDONG (FIG. 1:2)

Paleocene mammal-bearing strata in the Sanshui Basin belong to Formation I of the Buxin Group (Wang and Zhang, 1997). The only fossil mammal currently known from this rock unit was identified as ?*Hypsilolambda* sp. by Wang and Zhang (1997). The fossil-bearing beds are purplish red siltstone and grayish green fine sandstone intercalated with mudstone.

3. CHIJIANG BASIN, JIANGXI (FIG. 1:3)

The Chijiang Basin is located in the southern part of Jiangxi Province and is separated from the Nanx-
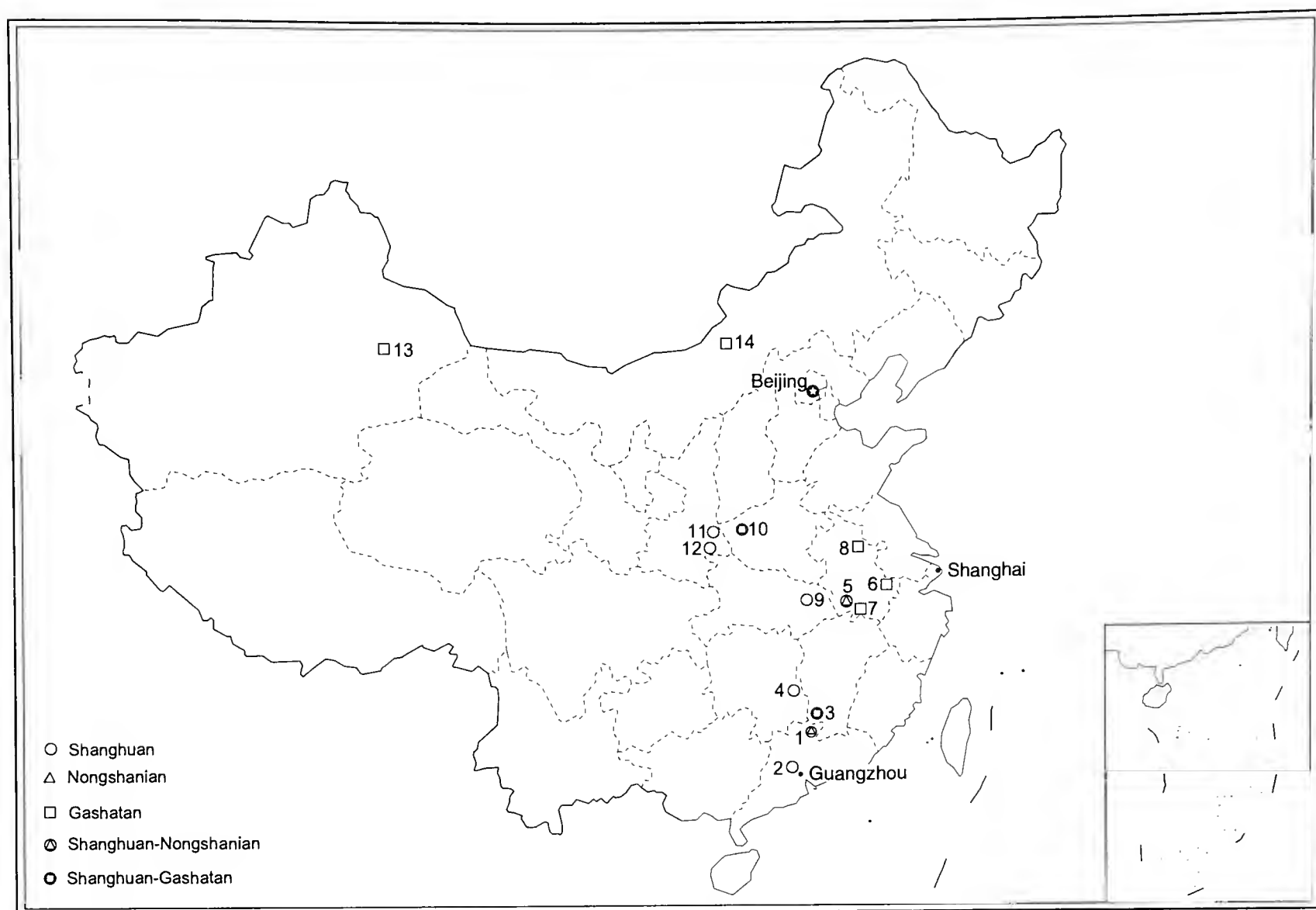
Fig. 1.—Sketch map showing the location of Chinese Paleocene basins. Numbers correspond to basin locations as follows: 1, Nanxiong Basin, Guangdong; 2, Sanshui Basin, Guangdong; 3, Chijiang Basin, Jiangxi; 4, Chaling Basin, Hunan; 5, Qianshan Basin, Anhui; 6, Xuancheng Basin, Anhui; 7, Tongling Basin, Anhui; 8, Jiashan Basin, Anhui; 9, Xinzhou Basin, Hubei; 10, Tantou Basin, Henan; 11, Shimen Basin, Shaanxi; 12, Shanyang Basin, Shaanxi; 13, Turfan Basin, Xinjiang; 14, Erlian Basin, Nei Mongol.

iong Basin only by the Nanling Mountains. Paleogene continental strata in this basin comprise the Shizikou Formation, the Chijiang Formation (including the Lannikeng and Wangwu members), and the Pinghu Formation, in ascending order (Tong et al., 1976, 1979). The Shizikou Formation disconformably overlies the Nanxiong Formation and is about 120 m in thickness. It is composed of mainly brick-red sandy mudstone intercalated with grayish green sandstone. The Chijiang Formation disconformably overlies the Shizikou Formation and is about 470 m thick in one section. Its lower part, the Lannikeng Member, comprises mainly purplish red mudstone and brick-red and grayish green sand-conglomerates, while its upper part, the Wangwu Member, consists of dominantly purplish red mudstone intercalated with grayish red and grayish green sandstone. The Pinghu Formation is composed of mainly purplish red pelitic sandstone and mudstone with intercalating yellowish green siltstone. Its thickness varies from 200 to 300 m. Tong

et al. (1976, 1979) suggested that the Shizikou and Chijiang formations are Paleocene in age, while the Pinghu Formation is early Eocene. However, the Pinghu Formation is also considered to be Paleocene in age in this paper.

4. CHALING BASIN, HUNAN (FIG. 1:4)

Paleocene rocks in the Chaling Basin have been known as the Zaoshi Formation, which disconformably overlies the Late Cretaceous Dainan Formation (Gao, 1975). It is over 53 m thick and consists of purplish red silty mudstone and mudstone intercalated with siltstone and fine sandstone. Most species of the fossil mammals from the Zaoshi Formation belong to taxa common in the early–middle Paleocene of South China (Wang, 1975).

5. QIANSHAN BASIN, ANHUI (FIG. 1:5)

The redefined Wanghudun and Doumu formations (Qiu et al., 1977) have been widely accepted for Paleocene strata in the Qianshan Basin (e.g.,

Zheng and Qiu, 1979; Chow and Zheng, 1980; Li and Ting, 1983; Russell and Zhai, 1987). The Wanghudun Formation, which is about 1800 m thick, disconformably overlies the Cretaceous Wanghe Formation and was subdivided into the Lower, Middle, and Upper members (Qiu et al., 1977). The Lower Member is composed of purplish red medium-fine sandstone intercalated with conglomerates and grayish white arkose sandstone. The Middle Member consists of mainly interbedded purplish red conglomerates, coarse sandstone, and fine sandstone. No fossil mammals have been recorded from this member. The Upper Member is the most fossiliferous unit in the formation, comprising purplish and brownish red fine sandstone intercalated with grayish white arkose sandstone. The Doumu Formation unconformably overlies the Wanghudun Formation and is about 600 m in total thickness. The lower part of the formation, the Lower Member, comprises thick, purplish red medium-fine sandstone intercalated with thin conglomerates and silty mudstone, while its upper part, the Upper Member, is composed of mainly interbedded thick conglomerates and sandstone (Qiu et al., 1977).

6. Xuancheng Basin, Anhui (Fig. 1:6)

Mesozoic and Cenozoic red beds in the Xuancheng Basin fall into two categories: the lower Xuannan Formation and the upper Shuangtasi Formation (original Shuangtasi Group). The Shuangtasi Formation unconformably overlies the Xuannan Formation (Qiu et al., 1977) and is composed of mainly purplish red and red silty mudstone and siltstone intercalated with conglomerates. Its thickness varies from 213 to 760 m. The age of the Xuannan Formation was determined as Late Cretaceous because of the presence of dinosaur egg shells. However, the Shuangtasi Formation was considered to be either late Paleocene (Qiu et al., 1977; Li and Ting, 1983) or early Eocene in age (Zheng and Qiu, 1979; Zheng and Huang, 1986).

7. Tongling Basin, Anhui (Fig. 1:7)

The red beds in the Tongling Basin were originally considered to be Cretaceous in age. In the 1980s, investigations by local geologists demonstrated the existence of Paleocene strata in this basin (Bureau of Geology and Mineral Resources of Anhui Province, 1987). Using the terminology from the neighboring Qianshan and Xuancheng basins, the local geologists divided the Paleocene red beds into the lower Doumu Formation and the upper Shuangtasi Formation on the basis of both litholog-

ical and paleontological evidence (Bureau of Geology and Mineral Resources of Anhui Province, 1987). The Doumu Formation consists of variegated fine-grained sandstone, siltstone intercalated with silty mudstone, and mudstone. It yields the conchostracan *Fushunograpta changzhouensis* and ostracods, but fossil mammals have not yet been recovered from this formation. The Shuangtasi Formation is composed of purplish red sandstone, siltstone, and mudstone intercalated with conglomerates and sandy conglomerates. Its thickness at the Meigeng section in Guichi County is 373 m. Some fossil mammals were collected from this formation, and these were recently described by Huang and Chen (1997).

8. Jiashan Basin, Anhui (Fig. 1:8)

The Jiashan Basin is another small basin with Paleocene continental deposits yielding fossil mammals, located in the eastern part of central Anhui. The only Paleocene mammal described to date from this basin is the mesonychid *Sinonyx jiashanensis* (Zhou et al., 1995). In their original description of the well-preserved holotype skull, Zhou et al. (1995) cited the Tujinshan Formation as the provenance of *Sinonyx jiashanensis*. According to the Regional Geology of Anhui Province (Bureau of Geology and Mineral Resources of Anhui Province, 1987), the Tujinshan Formation consists of mainly brick-red sandy conglomerates, arkose sandstone, siltstone, silty mudstone, and mudstone. It is over 542 m thick. In the lower part of this formation occur some intercalated basalts.

9. Xinzhou Basin, Hubei (Fig. 1:9)

The occurrence of Paleocene strata in the Xinzhou Basin was not demonstrated until 1983, when the emydid turtle *Anhuichelys xinzhouensis* was published (Chen, 1983). Subsequently, the presence of Paleocene strata in this basin was confirmed by the discovery of fossil mammals. This area is located at the base of the southwestern slopes of the Dabie Mountains, while the Qianshan Basin lies at the base of the southeastern slopes of this range. So far, no detailed stratigraphic division has been proposed in this area. The fossil-bearing beds in the Xinzhou Basin belong to the so-called "Donghu Group," which consists of purplish fine- to coarse-grained sandstones intercalated with conglomerates. The recent discovery of fossil vertebrates in the Xinzhou Basin indicates that the fossiliferous strata in this area are not equivalent to those attributed to the "Donghu Group" in other areas. As such, it will

probably become necessary to redefine the rock unit bearing the fossil vertebrates in the Xinzhou Basin. The unique radiometric date for the Chinese Paleocene, 61.63 ± 0.92 Ma, was obtained from basalt samples from this stratigraphic unit.

10. Tantou Basin, Henan (Fig. 1:10)

The Tantou Basin is a small basin in the eastern part of the Qinling Mountains area. It bears some early Tertiary strata, which have been divided into the Gaoyugou, Dazhang, and Tantou formations and an additional unnamed formation in ascending order by Tong and Wang (1980). The Gaoyugou Formation, which lies disconformably on the Late Cretaceous Qiuba Formation, is composed of mainly purplish red mudstone. In its lower part are some intercalated conglomerates, while some grayish green siltstone is intercalated in the upper part. The thickness of the Gaoyugou Formation has been measured as 302 m at the Gaoyugou section and 370 m at the Wangzhuang section. A few specimens of *Bemalambda* and mesonychids were collected from this formation (Tong and Wang, 1980). *Bemalambda* is currently known only from the Shanghu Formation and its correlatives in South China and the Qinling Mountains area.

The Dazhang Formation consists of predominantly interbedded dark red and grayish green mudstone and light gray marlstone. A layer of grayish green coarse sandstone is present at the bottom of this formation. The Dazhang Formation is about 104 m thick at the Gaoyugou section and about 375 m thick at the Tanyugou section. The fossil mammals from this formation were cited as Pastoralodontidae and Pseudictopidae by Tong and Wang (1980) and Russell and Zhai (1987), but these identifications must be reassessed based on our preliminary observations.

The Tantou Formation is mainly grayish green and gray mudstone, shale, marlstone, and oil-shale intercalated with sandstone. Its thickness has been measured as 136 m at the Gaoyugou section and over 458 m at the Tanyugou section (Tong and Wang, 1980). Tong and Wang (1980) cited the mammalian fossils found in this formation as Prodinoceratinae and Pantolambdodontidae (= Archaeolambdidae). The unnamed upper formation consists of brownish red or light yellow conglomerates, from which fossil mammals have yet to be recovered. Based on the fossil mammals collected from the lower three formations, Tong and Wang (1980) tentatively considered their age to be middle Paleocene, late Paleocene, and early Eocene, re-

spectively. However, Russell and Zhai (1987:49) suggested that the Tantou Formation "could be contemporary with the strata that furnished the Gashato or the Bayan Ulan faunas." Correlation of the mammal-bearing beds in the Tantou Basin has been hampered by the lack of formal description of the fossil mammals known from these rock units, but it is likely that all three formations yielding fossil mammals are Paleocene in age, representing the Shanghuan through the Gashatan. Correlation of these rock units with Paleocene strata in other Chinese basins will not be discussed further in this paper, pending formal description of the fossil mammals known from this basin.

11. Shimen Basin, Shaanxi (Fig. 1:11)

The Shimen Basin is one of the fault-controlled intermontane basins in the eastern part of the Qinling Mountains area. The Paleocene strata have been called the Fangou Formation, which unconformably overlies Precambrian rocks. The Fangou Formation is dominantly composed of brownish red sandy mudstones and mudstone intercalated with conglomerates. Its total thickness is about 170 m (Xue and Zhao, 1982).

12. Shanyang Basin, Shaanxi (Fig. 1:12)

The Shanyang Basin is another small intermontane basin in the same district as the Shimen Basin. The Paleocene strata, known as the Juanling Formation, consist of mainly yellowish red muddy siltstones and sandy mudstones intercalated with sandy conglomerates. Its thickness varies from 270 to about 300 m (Xue et al., 1987). Paleomagnetic and geochemical research in the Shanyang Basin indicates that the Juanling Formation was deposited under relatively hot and dry climatic conditions from 65 to 61 Ma BP (Xue et al., 1996).

13. Turfan Basin, Xinjiang (Fig. 1:13)

The Turfan Basin is a large basin in northwestern China, in which both Mesozoic and Cenozoic continental deposits are exposed. The Paleocene rock units in the Turfan Basin include the Taizicun Formation and the Dabu Formation. Because these two formations are exposed in different parts of the basin, their stratigraphic relationships cannot be demonstrated directly, but the fossil mammals from both formations suggest that they possibly represent two different stratigraphic levels (Zhai et al., 1978). The Taizicun Formation consists of purplish and brownish red arenaceous mudstone intercalated with grayish green fine sandstone. This formation is probably

fluvial in origin rather than lacustrine (Russell and Zhai, 1987). Its measured thickness varies from 30 to 65 m at different sections. The Dabu Formation is mainly purplish red and gray mudstone and light gray sandstone. Its thickness was measured as about 22 m at the Dabu section (Zhai et al., 1978). The age of the Taizicun Formation has been widely accepted as late Paleocene, and the mammalian fauna therefrom could be contemporary with those from the Gashato and Nomogen formations (Tong, 1978). Zhai (1978) regarded the Dabu Formation to be early Eocene in age, but our reconsideration suggests that it, too, is late Paleocene (see discussion below).

14. ERLIAN BASIN, NEI MONGOL (FIG. 1:14)

In the Erlian Basin, the Nomogen Formation was first proposed for Paleocene strata in the Nomogen area by Zhou et al. (1976). Meng et al. (1998) describe the mammal fauna from the basal part of the Bayan Ulan section, north of Haliut. These strata were previously called the Bayan Ulan Formation (Qi, 1979; Jiang, 1983; Li and Ting, 1983) or the Bayan Ulan beds of the Nomogen Formation (Qi, 1987, 1990), and have been frequently cited as early Eocene in age. Meng et al. (1998) suggest that "the Bayan Ulan beds and the Nomogen beds are stratigraphically equivalent" and consider the age of the

Bayan Ulan beds to be late Paleocene. However, they provided a note in brackets to indicate that the basal beds at the Bayan Ulan locality belong to the upper part of the Nomogen Formation. In this paper, we follow Meng et al. (1998) and use the Nomogen Formation to encompass both the strata of the typical Nomogen Formation and those comprising the basal part of the Bayan Ulan section, that is, the so-called Bayan Ulan beds. The Nomogen Formation consists of predominantly dark red sandy mudstone and muddy sandstone and is about 16 m thick at Haliut, the type section (Zhou et al., 1976). Rocks attributed to this formation at the Bayan Ulan section are brownish red sandstone, grayish green silty mudstone, and variegated mudstone (Qi, 1987). Qi (1990) distinguished the "Bayan Ulan beds" from the "Nomogen beds" on the basis of whether or not the concretions are rich in celestite, when he reported the discovery of *Pastoralodon lacustris* at Erden Obo in the Erlian Basin. Alternatively, this variation in celestite may only reflect facies differences.

Discussion in this paper is restricted to the rock units cited above and the faunas derived therefrom, although some other Chinese Paleogene beds may eventually prove to be Paleocene in age as well.

COMPOSITION OF CHINESE PALEOCENE MAMMAL FAUNAS

The Chinese Paleocene mammal record was reviewed by Li and Ting (1983) and Russell and Zhai (1987) in their synopses of Chinese and Asian Paleogene mammals and stratigraphy. Subsequently, new localities and new taxa have been published which have enriched our knowledge of Chinese Paleocene mammals and biostratigraphy. To date, 121 mammalian species have been named from the Chinese Paleocene (see Appendix). The mammalian record of Paleocene age in China comprises 81 genera in 27 families, representing 17 orders, although a few genera are considered as Order and/or Family incertae sedis. Chinese Paleocene mammals described since the publication of Russell and Zhai (1987) are briefly discussed here.

1. NANXIONG BASIN, GUANGDONG

One perissodactyl-like mammal, assigned to ?Phenacolophidae, and two species of insectivores have been reported from the Nanxiong Basin since Russell and Zhai's (1987) summary:

Insectivora
Lipotyphla
  Family indet.
    Carnilestes Wang and Zhai, 1995
      C. palaeoasiaticus Wang and Zhai, 1995
      C. major Wang and Zhai, 1995
Order indet.
  ?Phenacolophidae
    Radinskya McKenna, Chow, Ting, and Luo, 1989
      R. yupingae McKenna, Chow, Ting, and Luo, 1989

The two species of *Carnilestes* were reported from the Shanghu Formation on the basis of five specimens (Wang and Zhai, 1995), while the partial skull of *Radinskya* was collected from the Datang Member of the Nongshan Formation (McKenna et al., 1989). Russell et al. (1993:143) inaccurately reported that the Nongshan Formation "has produced a mammalian assemblage containing *Coryphodon* and *Prodinoceras*." In fact, neither *Coryphodon* nor

Prodinoceras has been recorded to date from the Nongshan Formation.

Lucas and Williamson (1995) suspected that the holotype of *Hukoutherium ambigum*, a left lower jaw, actually represents another genus, *Dissacusium*, which is based on an isolated upper molar. However, more nearly complete specimens of *Hukoutherium* from the Fangou Formation of the Shimen Basin indicate that these two genera are distinct (Qi and Huang, 1982).

2. SANSHUI BASIN, GUANGDONG

The only fossil mammal, a bemalambdid, from the Formation I of the Buxin Group was described by Wang and Zhang (1997).

> Pantodonta
> Bemalambdidae
> ?*Hypsilolambda* sp. (*in* Wang and Zhang, 1997)

3. CHIJIANG BASIN, JIANGXI

Two arctostylopids have been added to the faunal list of the Chijiang Formation in the Chijiang Basin:

> Arctostylopida Cifelli, Schaff, and McKenna, 1989
> Arctostylopidae
> *Bothriostylops* Zheng and Huang, 1986
> *B. notios* Zheng and Huang, 1986
> *B.* sp. (*in* Zheng and Huang, 1986)

Arctostylopidae were regarded as a family of Notoungulata for many years. Zheng and Huang (1986) also placed *Bothriostylops* in Notoungulata and transferred *Sinostylops progressus* from the Xuancheng Basin to their new genus as a distinct species, *Bothriostylops progressus* (Tang and Yan). Cifelli et al. (1989) proposed Arctostylopida as a new ordinal-level taxon for Arctostylopidae. Accordingly, *Bothriostylops* should be classified as a representative of Arctostylopida.

4. QIANSHAN BASIN, ANHUI

Eight species in three orders have been described in the past decade from Paleocene rocks of the Qianshan Basin, Anhui Province. Because some new taxa described in Wang's (1993) dissertation have not yet been formally published, they are listed here only in informal names.

> Anagalida
> Anagalidae
> *Eosigale* Hu, 1993

> *E. gujingensis* Hu, 1993
> *Qipania* Hu, 1993
> *Q. yui* Hu, 1993
> Mimotonida
> Mimotonidae
> *Mimotona lii* Dashzeveg and Russell, 1988
> Tillodontia
> Esthonychidae
> *Plethorodon* Huang and Zheng, 1987
> *P. chienshanensis* Huang and Zheng, 1987
> Pantodonta
> Pastoralodontidae
> *Altilambda*
> *A. yujingensis* Wang, Yu, and Li, 1992
> *A.* n. sp. (*in* Wang, 1993)
> ?Alcidedorbignyidae de Muizon and Marshall, 1992
> N. gen. and sp. (*in* Wang, 1993)
> New Family (*in* Wang, 1993)
> N. gen. and sp. (*in* Wang, 1993)
> Order and Family indet.
> *Wania* Wang, 1995
> *W. chowi* Wang, 1995

Of the species cited above, the two anagalids, *Altilambda yujingensis*, *Wania chowi*, and the new family of pantodonts came from the Upper Member of the Wanghudun Formation, while the new genus referred to ?Alcidedorbignyidae and *Plethorodon chienshanensis* were found in the upper part of the Lower Member of this formation. Another species of *Altilambda*, *A.* n. sp., was collected from the Doumu Formation. *Plethorodon* was originally referred to the ?Pantodonta by Huang and Zheng (1987). De Muizon and Marshall (1992:515) suggested that *Plethorodon* is not a pantodont and is probably a tillodont, a conclusion with which Wang (1993) agreed. Wang (1993) also transferred *Altilambda minor* from the Datang Member of the Nongshan Formation in the Nanxiong Basin (Tong, 1982) into his new genus as a distinct species. *Wania chowi* was originally referred to the family Zhelestidae in the order Mixotheridia by Wang (1995). At that time, Mixotheridia was thought by Nessov et al. (1994) to include Zhelestidae and Zalambdalestidae. More recently, Nessov et al. (1998) removed "zhelestids" from Mixotheridia and assigned them to Ungulatomorpha. Archibald (1996) further argued for a Late Cretaceous origin of "hoofed" mammals (Ungulatomorpha) on the basis of the Asian fossil evidence. In their paper, Nessov

et al. (1998) also argued that *Wania chowi* "is not a zhelestid but may have anagalidan affinities." Because determination of its phylogenetic position requires further study, *Wania chowi* is temporarily classified as Order and Family indeterminate.

5. Tongling Basin, Anhui

The mammalian fossils found in this basin were recently described by Huang and Chen (1997). All of the fossils were collected from the Shuangtasi Formation. They are:

  Arctostylopida
    Arctostylopidae
      Bothriostylops progressus (Tang and Yan, 1976)
  Pantodonta
    Pantolambdodontidae
      Archaeolambda sp., cf. *A. yangtzeensis* Huang, 1978
      Guichilambda zhaii Huang and Chen, 1997

6. Jiashan Basin, Anhui

This new locality for Paleocene mammals is located in the eastern part of central Anhui Province, at approximately 32°47′N, 117°50′E. Fossils of several kinds of mammals were collected from the Tujinshan Formation in that basin, but only a mesonychid skull has been described to date (Zhou et al., 1995).

  Mesonychia
    Mesonychidae
      Sinonyx Zhou, Zhai, Gingerich, and Chen, 1995
      S. jiashanensis Zhou, Zhai, Gingerich, and Chen, 1995

7. Shimen Basin, Shaanxi

A new anagalid species and two bemalambdid species from the Fangou Formation can be added to the faunal list for this basin.

  Anagalida
    Anagalidae
      Linnania
        L. qinlingensis Xue, 1986
  Pantodonta
    Bemalambdidae
      Bemalambda
        B. zhoui Xue, Zhang, Bi, Yue, and Chen, 1996
        B. sp., cf. *B. pachyoesteus* Chow, Chang, Wang, and Ting, 1973 (*in* Xue et al., 1996)

8. Shanyang Basin, Shaanxi

Xue et al. (1996) described a specimen of *Bemalambda* from the upper part of the Juanling Formation in this basin.

  Pantodonta
    Bemalambdidae
      Bemalambda
        B. sp., cf. *B. pachyoesteus* Chow, Chang, Wang, and Ting, 1973 (*in* Xue et al., 1996)

9. Erlian Basin, Nei Mongol

Bayan Ulan

The mammalian fossils from the Nomogen Formation in the Bayan Ulan area were first reported by Qi (1979), but no fossils were actually described at that time. The faunal list was also cited by Li and Ting (1983) and Russell and Zhai (1987). Only two taxa, *Lambdopsalis bulla* and *Tribosphenomys minutus*, have been thoroughly described (Miao, 1986, 1988; Meng and Wyss, 1994; Meng et al., 1994). The description of the fauna as a whole is provided by Meng et al. (1998). The fossil mammals now known from this locality provide further information regarding biostratigraphy, paleoecology, taphonomy, etc. Recently described mammal taxa from the Nomogen Formation are listed below.

  Lipotyphla
    Soricomorpha
      Nyctitheriidae
        Bayanulanius Meng, Zhai, and Wyss (1998)
          B. tenuis Meng, Zhai, and Wyss (1998)
  Insectivora
    Family indet.
      Sarcodon
        S. minor Meng, Zhai, and Wyss (1998)
    Palaeoryctoidea
      Gen. and sp. indet. (*in* Meng, Zhai, and Wyss, 1998)
    ?Leptictidae
      N. gen. and sp. Meng, Zhai, and Wyss (1998)
  Creodonta
    Hyaenodontidae
      Limnocyoninae
        Prolimnocyon Matthew, 1915

P. chowi Meng, Zhai, and Wyss (1998)

?Creodonta
    Family indet.
        Gen. and sp. indet. (*in* Meng, Zhai, and Wyss, 1998)

Carnivora
    ?Viverravidae
        cf. *Viverravus* sp. (*in* Meng, Zhai, and Wyss, 1998)

Mixodontia
    Eurymylidae
        Khaychina Dashzeveg and Russell, 1988
        ?*K. elongata* Dashzeveg and Russell, 1988

Rodentia
    Alagomyidae
        Tribosphenomys Meng, Wyss, Dawson, and Zhai, 1994
        T. minutus Meng, Wyss, Dawson, and Zhai, 1994

Mesonychia
    Mesonychidae
        Pachyaena
            P. sp. (*in* Meng, Zhai, and Wyss, 1998)

Perissodactyla
    Family indet.
        Gen. and sp. indet. (= ?*Lambdotherium* sp., cited by Russell and Zhai, 1987)

Khaychina elongata was originally described as a ?eurymylid from the Naran Member of the Naran-Bulak beds of Mongolia (Dashzeveg and Russell, 1988). The occurrence of this species at Bayan Ulan was reported by Meng et al. (1998). *Tribosphenomys minutus* was questionably referred to the rodent family Alagomyidae by Meng et al. (1994), but *Tribosphenomys* was excluded from Rodentia by Meng and Wyss (1994), who narrowly defined the order to include only its "crown clade." However, Dawson and Beard (1996) argued that *Alagomys* is a primitive rodent and pointed out that "the many similarities between *Alagomys* and *Tribosphenomys* support reference to a common clade." They also classified both genera in the family Alagomyidae.

Erden Obo

Qi (1990) reported this new locality for Chinese Paleocene mammals and described a pantodont species.

Pantodonta
    Pastoralodontidae Chow and Qi, 1978
        Pastoralodon lacustris Chow and Qi, 1978

Qi (1990) considered the strata bearing *P. lacustris* to be equivalent to the Bayan Ulan beds and of early Eocene age. More recent investigations suggest that the Bayan Ulan beds are late Paleocene in age (Meng et al., 1998).

In addition to discoveries of new taxa from various localities during the past decade, some workers have also revised the taxonomic positions of certain Chinese Paleocene mammal taxa, which, in some cases, may affect biostratigraphic correlations. These revisions can be summarized as follows:

1. Pantodonta: Lucas (1982) revised the composition of the order with little discussion. Some of his revisions were cited by Russell and Zhai (1987) in their summary of Asian Paleogene mammals and stratigraphy. After reexamining all Chinese noncoryphodontid pantodont specimens, Wang (1993) revised the classification of Chinese noncoryphodontid pantodonts in his unpublished Ph.D. dissertation. In contrast to Lucas' opinion that *Nanlingilambda* and *Convallisodon* are synonyms of *Archaeolambda* and *Pastoralodon*, respectively, Wang (1993) maintained *Nanlingilambda* and *Convallisodon* as distinct genera. In addition, Wang (1993) synonymized *Archaeolambda zhuguikengensis* with *A. speciosa*. Both of these forms were originally described as distinct species of *Dilambda* by Tong (1978, 1982). Wang (1993) also identified a specimen (IVPP V5044) described as *Archaeolambda* sp. by Tong (1979b) as *A. tabiensis* Huang (1977). He further referred a left lower jaw fragment with P_1–M_1 and M_3 (IVPP V5486b) from the original sample of *Convallisodon haliutensis* Chow and Qi (1978) to *C. convexus* Chow and Qi (1978), and reassigned the other specimen of *Convallisodon haliutensis*, a right maxilla with P^3–M^3 (IVPP V5486a), to *Pastoralodon* as a separate species. Lucas and Williamson (1995) considered a nearly complete sacrum, originally described as ?*Ectoconus* sp. by Zhou et al. (1977), as more likely pertaining to *Bemalambda*, but the different number of sacral vertebrae, four in ?*Ectoconus* and three in *Bemalambda* (Zhou et al., 1977), conflicts with their reassignment. To date, 25 named pantodont species, as well as four unnamed species, in six families have been described from the Paleocene of China.

2. Anagalidae: In addition to his description of two new anagalid genera and species, Hu (1993)

reviewed Chinese anagalid specimens. After detailed character analysis, he tentatively transferred *Chianshania* from Anagalidae to Astigalidae and excluded *Wanogale* and *Khashanagale* from Anagalidae. Lucas and Williamson (1995) suggested that the Chinese Paleocene mammals *Yuodon*, *Palasiodon*, and "Phenacodontidae gen. et sp. nov." (Zhou et al., 1977) from the Nanxiong Basin, were anagalids rather than condylarths. These fossils may not be hyopsodontid or phenacodontid condylarths as described by Chow et al. (1973) and Zhou et al. (1977), but, on the other hand, their dental morphology also differs substantially from that of anagalids according to Szalay and McKenna's (1971) and Hu's (1993) diagnoses of Anagalidae. Therefore, we temporarily maintain the original classification of these taxa.

3. Glires: Chinese Paleocene Glires have so far been recorded only from the Qianshan Basin in Anhui (Li, 1977), the Erlian Basin in Nei Mongol (Chow and Qi, 1978; Meng et al., 1998), and the Turfan Basin in Xinjiang (Tong, 1978). Li et al. (1987) proposed an ordinal rank taxon, Mimotonida, for Mimotonidae, and kept Eurymylidae in Mixodontia. The diagnostic characters of Mimotonidae were further clarified by C. Li (1989). However, Meng and Wyss (1994) recommended abandoning Eurymylidae, Eurymyloidea, Mimotonidae, and Mixodontia in favor of Glires incertae sedis. For the sake of simplicity, we continue to use the former names for these taxa. In addition, Dashzeveg and Russell (1988) transferred *Mimotona borealis* from the Nomogen Formation of Nei Mongol with doubt to their new genus, *Eomylus*, as a distinct species. Meng et al. (1998) reported the occurrence of *Eomylus borealis* in the Bayan Ulan local fauna and referred this species to *Eomylus* without reservation.

4. Arctostylopidae: This family has traditionally been referred to Notoungulata. However, Cifelli et al. (1989) compared the morphotype for arctostylopids with that for South American notoungulates and removed the Holarctic Arctostylopidae from Notoungulata. They placed Arctostylopidae in its own order, Arctostylopida. At the same time, they revised the classification of Arctostylopidae and named a new genus, *Gashatostylops*, with *Palaeostylops macrodon* as its type species, systematic actions with which Huang and Chen (1997) disagreed. *Gashatostylops macrodon* occurs in the Nomogen Formation in China (Chow and Qi, 1978; Cifelli et al., 1989; Meng et al., 1998) and in the Gashato Formation in Mongolia (Matthew et al., 1929; Cifelli et al., 1989).

5. Mesonychidae: This family has been variously assigned to the order "Condylarthra" or to its own order as Mesonychia or Acreodi. Li and Ting (1983) and Russell and Zhai (1987) classified mesonychids as members of Condylarthra. Because of the possible close relationship between mesonychids and cetaceans, a separate ordinal-level designation for mesonychids is becoming increasingly accepted. Accordingly, all Chinese Paleocene mesonychids should be reassigned to the order Mesonychia Van Valen (1966) (= McKenna's [1975] concept of Acreodi Matthew). However, Meng et al. (1998) continue to use Condylarthra as an ordinal rank taxon for Mesonychidae. In addition, they combined ?*Dissacus* sp. and *Plagiocristodon serratus* into a single species, *Dissacus serratus* (Chow and Qi), based on well-preserved specimens collected from the Nomogen Formation at Bayan Ulan (Meng et al., 1998).

6. Ting and Zheng (1989) reevaluated the affinities of *Interogale* from the Datang Member of the Nongshan Formation in the Nanxiong Basin and *Anchilestes* from the Lower Member of the Wanghudun Formation in the Qianshan Basin, and assigned both taxa to the order Tillodontia. The *Interogale* jaws bear several features similar to those of tillodonts, and these may indicate its tillodont affinities. However, the morphology of both the upper and lower dentition of *Anchilestes* is distinct from that of tillodonts, providing little evidence to support a special relationship to tillodonts. *Anchilestes* was originally referred to Zalambdalestidae within Anagalida (Qiu and Li, 1977), but its dental morphology is dissimilar to that of zalambdalestids. Kielan-Jaworowska (1984:109) stated that "in molars of *Zalambdalestes* and *Barunlestes* the trigonids are greatly reduced in length with respect with the talonids," which is not the case in *Anchilestes*. At present, we classify *Anchilestes* as Eutheria incertae sedis.

7. *Petrolemur* was originally referred to Adapidae by Tong (1979a) and was subsequently considered to be nonprimate (Russell and Gingerich, 1980; Szalay, 1982). However, Szalay and Li (1986) hinted that *Petrolemur* and the Eocene *Lushius* may represent a third branch of early primates in Asia. Currently, we tentatively accept *Petrolemur* as a representative of Primates, but we classify it as Family incertae sedis. Szalay and Li (1986) combined *Diacronus anhuiensis* Xu (1976) and *Decoredon elongetus* Xu (1977) from the Upper Member of the Wanghudun Formation into a single species, *Decoredon anhuiensis*, and proposed it as "the old-

est recognized member of euprimates, either an omomyid or a member of the common stock which gave rise to Adapidae and Omomyidae" (Szalay and Li, 1986:387). This assignment has received little support and was considered to be questionable (Rose et al., 1994) or unlikely (Gingerich et al., 1991; K. C. Beard, personal communication). It seems better to leave this species as Order and Family incertae sedis at present.

Correlation of the Chinese mammal-bearing Paleocene with the North American Paleocene suggests that the Paleocene/Eocene boundary in China is stratigraphically higher than many previous workers have believed (see discussion below). Therefore, it seems likely that the mammalian faunas collected from the Pinghu Formation in the Chijiang Basin in Jiangxi, the Dabu Formation in the Turfan Basin in Xinjiang, and the Nomogen Formation in the Erlian Basin in Nei Mongol are late Paleocene faunas. Of these faunas, the Bayan Ulan local fauna is updated by Meng et al. (1998), including description of some newly recorded taxa. The faunas from the Pinghu Formation and the Dabu Formation were re-
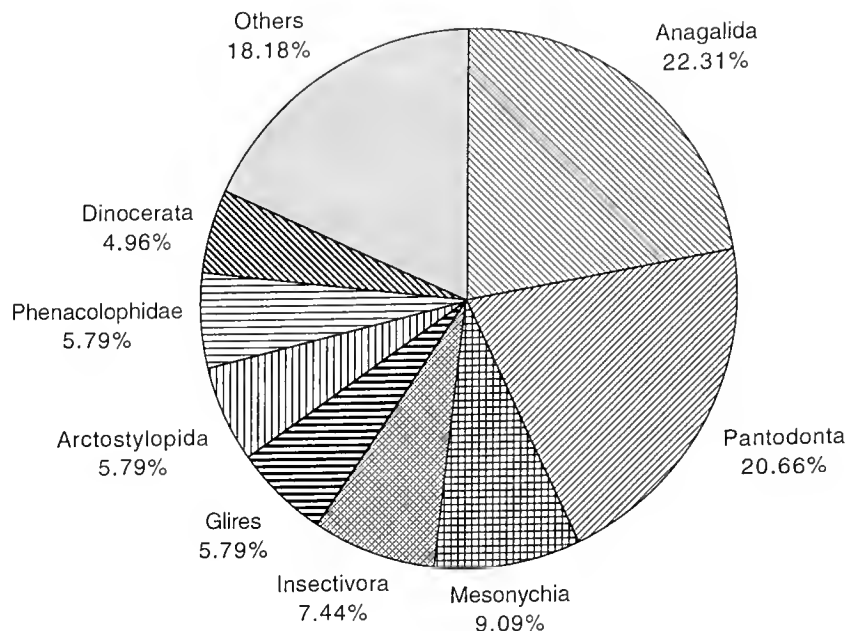

Fig. 2.—Pie chart showing the general taxonomic composition of Chinese Paleocene mammal faunas. Calculations of percentages for each taxon are based upon named species.

viewed by Russell and Zhai (1987), including recent systematic revisions.

The general taxonomic composition of Chinese Paleocene mammal faunas can be shown by a pie chart (Fig. 2).

GEOLOGICAL DISTRIBUTION AND BIOSTRATIGRAPHY OF CHINESE PALEOCENE MAMMALS

On the basis of the mammalian fossil record then available, previous researchers have proposed correlations of Paleocene strata within China. They considered that the Shanghu, Shizikou, and Wanghudun formations were correlatives and correlated the Nongshan Formation with the Chijiang and Doumu formations (South China "Red Beds" Research Group, 1977; Zheng and Qiu, 1979; Li and Ting, 1983; Ting, 1995, 1998). Meanwhile, both the Zaoshi Formation and the Fangou Formation were correlated to the Shanghu Formation (Xue and Zhao, 1982; and references cited above). Ting (1995, 1998) further correlated the lower and upper parts of the Shanghu Formation with the Lower and Upper members of the Wanghudun Formation, respectively, and the Zhuguikeng and Datang members of the Nongshan Formation with the Lannikeng and Wangwu members of the Chijiang Formation, and with the Lower and Upper members of the Doumu Formation, respectively. Regarding upper Paleocene strata, the Taizicun Formation and the Nomogen Formation were thought to be possible correlatives (Zhou et al., 1976) and the faunas from these formations were considered to be the same

age as the Gashato fauna (Zhou et al., 1976; Tong, 1978; Zhai et al., 1978; Russell and Zhai, 1987). The correlation of certain other Chinese Paleocene strata has been disputed, due to different interpretations of the stratigraphic significance of fossils derived therefrom.

Chinese Paleocene mammals come from many stratigraphic horizons in geographically and geologically disparate basins. Many mammal species, and even genera, have been reported from only a single basin, which is possibly caused by either or both of the following reasons. First, most Chinese Paleocene basins, especially relatively early ones, are small. They were not predominantly controlled by a single large-scale tectonic structure. Thus, paleoenvironmental conditions may have varied substantially among these basins, which resulted in the high diversity and endemism of mammals living there. Second, because virtually all Chinese Paleocene strata are not so abundantly fossiliferous, most Chinese Paleocene mammal species are based on a single specimen. Some of the specimens on which these mammal species are based are poorly preserved or fragmentary. In cases such as these, it can

be virtually impossible to determine whether morphological differences between specimens from different basins represent intraspecific variation as opposed to species-level or even generic-level taxonomic differences. Nevertheless, the extremely endemic pattern of distribution currently reported for Chinese Paleocene mammal species precludes the possibility of correlating Paleocene strata between different basins using species-level taxa. In this paper, correlation of the Chinese Paleocene is based primarily on taxa at generic rank. The stratigraphic and geographic distributions of some fossil mammals of significance for correlation of the Chinese

Paleocene are given in Figure 3. For colleagues who are not familiar with the Chinese mammal-bearing Paleocene, we will discuss the stratigraphic occurrences of some of these fossil mammals in more detail.

1. *Bemalambda* is among the most common mammals in the Chinese Paleocene. *Bemalambda* fossils have been described from six basins: the Nanxiong Basin in Guangdong, the Chijiang Basin in Jiangxi, the Chaling Basin in Hunan, the Qianshan Basin in Anhui, and the Shimen and Shanyang basins in Shaanxi. Relatively numerous *Bemalambda* specimens have been collected from the Nanx-

BASINS	A				B	C				D	E					F	G	H	I	J		K
STRATA	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Bemalambda	+	+				+				+	+	+						+	+			
Hypsilolambda					?					+												
Harpyodus							+					+										
Archaeolambda		+	+					+							+	+	+			+		
Altilambda				+								+			+							
Pastoralodon																						+
Coryphodon																					+	
Linnania	+																	+				
Huaiyangale				?								+										
Hsiuannania							+							+	+	+						
Astigale		+								+												
Paranictops												+										
Allictops														+								
Haltictops				+																		
Pseudictops							?													+		+
Yantanglestes		+		+							+											
Hukoutherium	+																	+				
Dissacus							?			+						+						+
Pappictidops		+										+										
Asiostylops							+															
Bothriostylops								+								+	+					
Sinostylops														+								
Palaeostylops																						+
Prodinoceras									+											+	+	+
Archaeoryctes							+					+										

Fig. 3.—Areal and stratigraphic distribution of some Paleocene mammal genera in China. All genera known to occur in more than one basin are listed here. Because of their significance in correlation, certain genera known only from a single basin are also listed. Capitalized letters refer to individual basins as follows: A, Nanxiong Basin, Guangdong; B, Sanshui Basin, Guangdong; C, Chijiang Basin, Jiangxi; D, Chaling Basin, Hunan; E, Qianshan Basin, Anhui; F, Xuancheng Basin, Anhui; G, Tongling Basin, Anhui; H, Shimen Basin, Shaanxi; I, Shanyang Basin, Shaanxi; J, Turfan Basin, Xinjiang; K, Erlian Basin, Nei Mongol. Within individual basins, stratigraphic rock units are distinguished by the following numerals: 1, Lower–middle part of the Shanghu Formation; 2, Upper part of the Shanghu Formation; 3, Zhuguikeng Member of the Nongshan Formation; 4, Datang Member of the Nongshan Formation; 5, Formation I of the Buxin Group; 6, Shizikou Formation; 7, Lannikeng Member of the Chijiang Formation; 8, Wangwu Member of the Chijiang Formation; 9, Pinghu Formation; 10, Zaoshi Formation; 11, Lower Member of the Wanghudun Formation; 12, Lower part of the Upper Member of the Wanghudun Formation; 13, Upper part of the Upper Member of the Wanghudun Formation; 14, Lower Member of the Doumu Formation; 15, Upper Member of the Doumu Formation; 16, Shuangtasi Formation; 17, Shuangtasi Formation; 18, Fangou Formation; 19, Juanling Formation; 20, Taizicun Formation; 21, Dabu Formation; 22, Nomogen Formation. The record of *Archaeoryctes* cited from the upper part of the Upper Member of the Wanghudun Formation in the Qianshan Basin is based on unpublished specimens.

iong, Chijiang, Chaling, and Shimen basins. In the Nanxiong Basin, *B. nanhsiungensis* and *B. pachyoesteus* occur in the lower (but not the lowest) through the upper fossil-bearing beds of the Shanghu Formation, while *B. crassa* occurs at the uppermost fossil-bearing bed in that formation (Zhou et al., 1977). *Bemalambda nanhsiungensis* was also recorded from the Zaoshi Formation in the Chaling Basin, where it occurs with another bemalambdid, *Hypsilolambda* (Wang, 1975). A fourth species, *B. shizikouensis*, occurs in the Shizikou Formation in the Chijiang Basin (Wang and Ding, 1979). Bemalambdids are relatively uncommon in the Qianshan Basin. *Bemalambda* sp. was reported from the upper part of the Lower Member of the Wanghudun Formation (Huang, 1978), and a newly collected lower molar from the lower part of the Upper Member of the Wanghudun Formation has been tentatively identified as *Bemalambda* sp., cf. *B. crassa*. Xue et al. (1996) described a new species of *Bemalambda*, *B. zhoui*, from the Fangou Formation in the Shimen Basin, and also identified some specimens from both the Fangou Formation in the Shimen Basin and the Juanling Formation in the Shanyang Basin as *Bemalambda* sp., cf. *B. pachyoesteus*.

2. *Harpyodus*, a primitive pantodont, was reported from both the Chijiang and Qianshan basins. The type species, *H. euros*, was recorded from the lower part of the Upper Member of the Wanghudun Formation (Qiu and Li, 1977), while another species, *H. decorus*, was recovered from the upper part of the Lannikeng Member of the Chijiang Formation (Wang, 1979; Tong et al., 1979). The latter appears a little more derived than the former (Wang, 1993).

3. *Altilambda*, a pastoralodontid pantodont, occurs in both the Nanxiong and Qianshan basins. *Altilambda pactus*, the type species, was reported from the Upper Member of the Wanghudun Formation and the Datang Member of the Nongshan Formation (Chow and Wang, 1978). More recent work reveals that in the Qianshan Basin *Altilambda* ranges from the Upper Member of the Wanghudun Formation to the Upper Member of the Doumu Formation (Wang, 1993). The specimen referred to *A. pactus* by Chow and Wang (1978) is a left lower jaw fragment with poorly preserved M_{1-2} (V5229) from the Nongshan Formation in the Nanxiong Basin. The fact that a new species of *Altilambda* has been recorded from a higher stratigraphic level and the lower dentition of one species of *Altilambda* is not clearly distinguishable from that of other species of this genus (Wang, 1993) raises doubt regarding the attribution of the Nanxiong specimen to *Alti-*

lambda pactus. Another pastoralodontid genus, *Pastoralodon*, has been reported only from the Nomogen Formation of the Erlian Basin, Nei Mongol (Chow and Qi, 1978). It is obviously more advanced than *Altilambda* and probably represents a younger pastoralodontid genus.

4. *Archaeolambda* has a relatively wide distribution in the Paleocene of China. It has been found in six basins: the Nanxiong, Chijiang, Qianshan, Xuancheng, Tongling, and Turfan basins. The type specimen of *Archaeolambda tabiensis* was described from the Upper Member of the Doumu Formation (Huang, 1977). Wang (1993) allocated a right lower jaw from the Wangwu Member of the Chijiang Formation to this species; this specimen had previously been described as *Archaeolambda* sp. by Tong (1979b). *Archaeolambda speciosa* (= *Dilambda zhuguikengensis* Tong, 1982) and *Archaeolambda* sp. 1 were reported from the Zhuguikeng Member of the Nongshan Formation (Tong, 1982; Wang, 1993) and the Lannikeng Member of the Chijiang Formation, respectively (Tong, 1979b; Wang, 1993). The specimens of *Archaeolambda* from the Shuangtasi Formation in the Xuancheng Basin and the Taizicun Formation in the Turfan Basin were reported as *A. yangtzeensis* (Huang, 1978) and *A. speciosa* (= *Dilambda speciosa* Tong, 1978), respectively. Huang and Chen (1997) recently reported *A.* sp., cf. *A. yangtzeensis* from the Shuangtasi Formation in the Tongling Basin.

5. Anagalidae are among the most common taxa in the Paleocene of China, but only a few genera have been found in more than one basin. *Linnania* is an anagalid genus reported from both the Nanxiong and Shimen basins. The type species of *Linnania*, *L. lofoensis*, was collected from the middle fossil bed of the Shanghu Formation (Zhou et al., 1977), while the other species, *L. qinlingensis*, was recovered from the Fangou Formation in the Shimen Basin (Xue, 1986). Another anagalid genus, *Hsiuannania*, has a wider distribution than *Linnania* and other genera. It has been reported from three basins: the Qianshan, Xuancheng, and Chijiang basins. The type species, *H. maguensis*, was recorded from the Shuangtasi Formation in the Xuancheng Basin (Xu, 1976), whereas *H. minor* was recovered from the upper part of the Lannikeng Member of the Chijiang Formation (Ding and Zhang, 1979). In the Qianshan Basin, fossils of *Hsiuannania* have been recovered from both the Lower (*H. tabiensis*) and Upper (*H.* sp.) members of the Doumu Formation (Xu, 1976). *Huaiyangale* is another anagalid genus reported from two basins. *Huaiyangale*

chianshanensis, the type species, was collected from the lower part of the Upper Member of the Wanghudun Formation, together with an undetermined specimen of the genus (Xu, 1976), while the other species, cf. *H. leura*, was recovered from the Datang Member of the Nongshan Formation (Ding and Tong, 1979). However, as Ding and Tong (1979) pointed out, the specimens of cf. *H. leura* are similar to those of *Huaiyangale*, but the poor preservation of these specimens precludes the undoubted attribution of this species to *Huaiyangale*.

6. Astigalidae have been reported only from the upper fossil-bearing beds of the Shanghu Formation in the Nanxiong Basin and the upper part of the Lower Member of the Wanghudun Formation in the Qianshan Basin, respectively (Xu, 1976; Zhang and Tong, 1981; Hu, 1993). This family contains five species in three genera, of which only one genus, *Astigale*, occurs in both basins (Zhang and Tong, 1981).

7. Pseudictopidae have been recorded in five basins in China, including the Nanxiong, Chijiang, Qianshan, Turfan, and Erlian basins, but only one genus, *Pseudictops*, has been reported from more than one basin. The Qianshan Basin has yielded the most pseudictopid taxa reported from the Paleocene in China. The pseudictopids *Anictops tabiepedis* and *Paranictops majuscula* are derived from the lower part of the Upper Member of the Wanghudun Formation (Qiu, 1977), while *Cartictops canina* and *Allictops inserrata* were collected from the upper part of the Lower Member of the Wanghudun Formation and the Lower Member of the Doumu Formation, respectively (Qiu, 1977; Qiu and Li, 1977; Ding and Tong, 1979). Two species of *Haltictops*, *H. mirabilis* and *H. meilingensis*, have been reported from the Datang Member of the Nongshan Formation (Ding and Tong, 1979). Cf. *Pseudictops tenuis* from the upper part of the Lannikeng Member of the Chijiang Formation is the only pseudictopid recorded in the Chijiang Basin (Ding and Tong, 1979; Ding and Zhang, 1979; Tong et al., 1979). It is more primitive than *P. lophiodon* from Gashato and may not be congeneric with the latter (Ding and Tong, 1979; Ding and Zhang, 1979). *Pseudictops chaii* and *P. lophiodon* have been reported from the Taizicun Formation of the Turfan Basin in Xinjiang and the Nomogen Formation of the Erlian Basin in Nei Mongol, respectively (Chow and Qi, 1978; Tong, 1978; Meng et al., 1998). Evidence is insufficient to clarify whether *P. chaii* is conspecific with *P. lophiodon* or not, but these forms are certainly

more similar to each other than to any other pseudictopids.

8. Mesonychidae are widely distributed in most Chinese Paleocene basins. Many mesonychid species have been based on poorly preserved specimens, creating doubt regarding the validity and systematic position of such taxa. *Yantanglestes* has been reported from both the Nanxiong and Qianshan basins. The type species, *Y. conexus*, was recovered from the upper part of the Lower Member of the Wanghudun Formation in the Qianshan Basin (Yan and Tang, 1976; Ideker and Yan, 1980). In the Nanxiong Basin, two species of the genus, *Y. feiganensis* and *Y. datangensis*, have been reported from the Shanghu Formation and the Datang Member of the Nongshan Formation, respectively (Wang, 1976; Zhou et al., 1977). Two species of *Hukoutherium*, *H. ambigum* and *H. shimenensis*, were recorded from the lower part of the Shanghu Formation in the Nanxiong Basin and the Fangou Formation in the Shimen Basin (Zhou et al., 1977; Qi and Huang, 1982). *Dissacus* has been reported from three basins: *D. rotundus* from the Zaoshi Formation in the Chaling Basin (Wang, 1975; Ting and Li, 1987), *D. magushanensis* from the Shuangtasi Formation in the Xuancheng Basin (Yan and Tang, 1976), and *D. serratus* from the Nomogen Formation in the Erlian Basin (Meng et al., 1998). *Dissacus* possibly existed in the Lannikeng Member of the Chijiang Formation in the Chijiang Basin (Zhang et al., 1979; Ting and Li, 1987). *Dissacus rotundus* has been considered to be similar to *D. navajovius* and *D. europaeus* (Wang, 1975) but more primitive (Ting and Li, 1987).

9. *Pappictidops*, the only named carnivore genus known from the Paleocene in China, has been recorded in both the Nanxiong and Qianshan basins. Two species of *Pappictidops*, *P. acies*, and *P. obtusus*, were described from the upper part of the Shanghu Formation (Wang, 1978), while the type species, *P. orientalis*, was recovered from the lower part of the Upper Member of the Wanghudun Formation (Qiu and Li, 1977).

10. Arctostylopidae have been reported in four basins. Most genera have been recovered only from a single basin. *Asiostylops* is based on a specimen from the upper part of the Lannikeng Member of the Chijiang Formation in the Chijiang Basin (Tong et al., 1979; Zheng, 1979b). It has been considered to be the most primitive known arctostylopid (Zheng, 1979b; Cifelli et al., 1989). *Bothriostylops* is the only arctostylopid genus recorded in three basins. The type species, *B. notios*, was reported from

the Wangwu Member of the Chijiang Formation in the Chijiang Basin (Zheng and Huang, 1986), while the other species, *B. progressus*, occurs in the Shuangtasi Formation of both the Xuancheng Basin (Tang and Yan, 1976; Zheng and Huang, 1986) and the Tongling Basin (Huang and Chen, 1997). *Bothriostylops progressus* is thought to be more advanced than *B. notios* (Zheng and Huang, 1986). Another genus, *Sinostylops*, has been reported from the Upper Member of the Doumu Formation in the Qianshan Formation (Tang and Yan, 1976) and is considered to be closely related to *Bothriostylops* by Cifelli et al. (1989). *Palaeostylops* from the Nomogen Formation of the Erlian Basin is among the most common taxa in the fauna from this formation (Chow and Qi, 1978; Meng et al., 1998). It is the most derived Chinese Paleocene arctostylopid (Zheng and Huang, 1986; Cifelli et al., 1989).

11. *Prodinoceras* is a uintathere occurring in relatively late Paleocene strata in China. *Prodinoceras lacustris* from the Pinghu Formation in the Chijiang Basin is the only species known from the Paleocene of South China (Tong, 1979c; Schoch and Lucas, 1985). Several species of *Prodinoceras* have been described from the Taizicun Formation in the Turfan Basin (Chow, 1960; Tong, 1978; Schoch and Lucas, 1985), while another species, *P. xinjiangensis*, has been reported from both the Dabu Formation in the Turfan Basin and the Nomogen Formation in the Erlian Basin (Zhai, 1978; Schoch and Lucas, 1985; Meng et al., 1998).

12. Although a newly collected specimen of the didymoconid genus *Archaeoryctes* from the Qianshan Basin has not yet been described, it possibly provides some new evidence for correlation. Therefore, the occurrence of the genus in China will be discussed here. The type species of this genus, *A. notialis*, has been reported from the middle of the Lannikeng Member of the Chijiang Formation (Tong et al., 1979; Zheng, 1979a). Recently, a well-preserved didymoconid skull was recovered from the upper part of the Upper Member of the Wanghudun Formation. It is currently identified as *Archaeoryctes* sp., but this specimen is very similar to or even conspecific with *A. notialis* Zheng.

Of all the Chinese Paleocene basins, the Nanxiong, Qianshan, Chijiang, and Erlian basins have yielded particularly important records of fossil mammals. The first three basins mainly produce fossil mammals spanning the early–middle Paleocene, while the fauna from Paleocene strata in the Erlian Basin documents relatively later Paleocene faunas. The records from these basins were used as

a baseline in correlating the Chinese mammal-bearing Paleocene. Figure 4 lists the biostratigraphically significant fossil mammals from the Nanxiong, Qianshan, and Chijiang basins, which aid in correlating lower–middle Paleocene strata in China.

On the basis of the mammalian fossil record from the Nanxiong, Qianshan, and Chijiang basins, we tentatively correlate the boundary between the Shanghu and Nongshan formations (Nanxiong Basin) with that between the Shizikou and Chijiang formations (Chijiang Basin) with the middle of the Upper Member of the Wanghudun Formation (Qianshan Basin). The mammalian faunas from strata below this boundary are dominated by *Bemalambda*, while faunas from strata above the boundary are characterized by the co-occurrence of *Archaeolambda* and *Altilambda*, without *Bemalambda*. Such a correlation first appeared in Wang's (1993) dissertation, with which Tong et al. (1995) agreed. Provisional correlation of the lower part of the Upper Member of the Wanghudun Formation with the uppermost fossil-bearing bed in the Shanghu Formation (see Zhou et al., 1977) is also proposed here. Because of insufficient fossil evidence, we only provisionally accept correlation of the Upper Member of the Doumu Formation with both the Datang Member of the Nongshan Formation and the Wangwu Member of the Chijiang Formation. Because of the extreme endemism of Paleocene mammal species or even genera in China, this correlation is only weakly supported at present. Nevertheless, the general pattern of the mammalian faunas from these basins suggests that such a correlation is reasonable.

The mammalian fossils from the Zaoshi Formation in the Chaling Basin were described by Wang (1975). Gao (1975) discussed the fauna from this formation and considered some of the mammal taxa to be more advanced than closely related forms from the lower part of the Shanghu Formation, which led to correlation of the Zaoshi Formation with the middle–upper part of the Shanghu Formation and its correlatives.

The Formation I of the Buxin Group in the Sanshui Basin, Guangdong, yielding only ?*Hypsilolambda* sp., was thought to be Paleocene in age (Wang and Zhang, 1997). Because *Hypsilolambda* has only been reported from the Zaoshi Formation (Wang, 1975) and Bemalambdidae are restricted to the Shanghu Formation and its correlatives, it seems reasonable to correlate the Formation I of the Buxin Group with the Zaoshi Formation and its correlatives.

Qianshan, Anhui			Nanxiong, Guangdong			Chijiang, Jiangxi		
						Pinghu Fm.		*Prodinoceras lacustris*
Doumu Fm.	Upper M.	*Archaeolambda tabiensis* *Hsiuannania* sp. *Altilambda* sp. nov. *Sinostylops promissus*	Nongshan Fm.	Datang M.	*Altilambda pactus* *Haltictops mirabilis* *Yantanglestes datangensis* cf. *Huaiyangale leura*	Chijiang Fm.	Wangwu M.	*Archaeolambda tabiensis* *Bothriostylops notios* *Allostylops periconotus*
	Lower M.	*Hsiuannania tabiensis* *Allictops inserrata*		Zhuguikeng M.	*Archaeolambda speciosa*		Lannikeng M.	*Asiostylops spanios* *Hsiuannania minor* cf. *Pseudictops tenuis* *Archaeoryctes notialis* *Harpyodus decorus*
Wanghudun Fm.	Upper M.	*Archaeoryctes* sp., cf. *A. notialis* *Altilambda pactus* *Bemalambda* sp., cf. *B. crassa* *Huaiyangale chianshanensis* *Harpyodus euros* *Pappictidops orientalis* *Anictops tabiepedis* *Paranictops majuscula*	Shanghu Fm.	Upper	*Bemalambda crassa* *B. nanhsiungensis* *Lofochaius brachyodus* *Pappictidops acies* *Astigale nanxiongensis*	Shizikou Fm.		*Bemalambda shizikouensis*
	Middle M.			Lower-Middle	*Bemalambda nanhsiungensis* *B. pachyoesteus* *Linnania lofoensis* *Yantanglestes feigangensis* *Disssacusium ambigum*			
	Lower M.	*Bemalambda* sp. *Astigale wanensis* *Yantanglestes conexus* Bemalambdidae indet.						

Fig. 4.—Stratigraphic distribution of selected Paleocene mammal taxa in the Qianshan, Nanxiong, and Chijiang basins, South China. The taxa are thought to be significant for correlation of the Chinese Paleocene. All of the taxa listed here are cited at the species level, but the correlation is actually based on generic taxa because of the extremely restricted distribution of Paleocene mammal species in China.

The Fangou Formation in the Shimen Basin, Shaanxi Province, has yielded four genera of Paleocene mammals (Qi and Huang, 1982; McKenna et al., 1984; Xue, 1986; Xue et al., 1996) and was correlated to the Shanghu, the Shizikou, the Zaoshi, and the Wanghudun formations (Xue and Zhao, 1982). According to Xue and Zhao (1982), all of the fossil mammals comprising this local fauna came from relatively high in the Fangou Formation. Of the four genera, two, *Linnania* and *Hukoutherium*, are known only from the middle part of the Shanghu Formation (Zhou et al., 1977) and one, *Bemalambda*, is restricted to the Shanghu Formation and its correlatives. It is likely that the fossil-bearing beds of the Fangou Formation are correlative with the middle part of the Shanghu Formation, but there is no fossil evidence bearing on whether or not the Fangou Formation also has strata correlative with the lower and upper parts of the Shanghu Formation. It seems possible to correlate the lower part of the Fangou Formation with the lower part, at least partly, of the Shanghu Formation because of the high stratigraphic position of the known fossiliferous bed.

The only fossil mammal described to date from the Juanling Formation in the Shanyang Basin is identified as *Bemalambda* sp., cf. *B. pachyoesteus* (Xue et al., 1996). This fossil can only suggest a rough correlation of the Juanling Formation with the Shanghu Formation in the Nanxiong Basin, but paleomagnetic results from the Juanling Formation (Xue et al., 1994, 1996) and the Shanghu Formation (Zhao et al., 1991) indicate that the Juanling Formation can be correlated with the entire Shanghu Formation. Both formations comprise strata spanning the duration from Chron 29r through Chron 27r or 27n (Zhao et al., 1991; Xue et al., 1994, 1996).

Although the mammal fossils collected from the Xinzhou Basin have not yet been described, we would still like to discuss the correlation of the fossil-bearing levels in this basin because of the unique radiometric date obtained there. In the Xinzhou Basin, two fossil-bearing horizons have been recog-

nized. So far, only four species of fossil mammals have been collected from these beds. Of these, two came from the upper bed, while the others were found in the lower bed. One of the species from the upper bed is provisionally identified as cf. *Anictops* sp., a pseudictopid also known from the lower part of the Upper Member of the Wanghudun Formation in the Qianshan Basin, while the other species is very similar to or even conspecific with *Paranictops majuscula*, which was also recovered from the lower part of the Upper Member of the Wanghudun Formation in the Qianshan Basin. Both taxa suggest a tentative correlation of the upper fossil-bearing bed in the Xinzhou Basin with the lower part of the Upper Member of the Wanghudun Formation in the Qianshan Basin.

Younger Paleocene strata occur mainly in North China. The Nomogen Formation in the Erlian Basin has yielded the most diverse assemblage of fossil mammals from this interval in China. The mammalian fauna from this formation includes Dinocerata (absent in faunas from the Nongshan Formation and its correlatives) and species of Pseudictopidae, Pastoralodontidae, and Arctostylopidae that are more derived than species representing these groups from the Nongshan Formation and its correlatives. A true rodent (*Tribosphenomys*) and a species of the hyaenodontid creodont genus *Prolimnocyon* also occur in this fauna. Evidence from the fossil mammals suggests that the Nomogen Formation is younger than the Nongshan Formation and its correlatives. The occurrence in the Nomogen Formation of quite a few species or genera shared with the Mongolian Gashato fauna indicates correlation of the Nomogen Formation with the strata bearing the Gashato fauna in Mongolia.

The local faunas from the Taizicun Formation in the Turfan Basin, Xinjiang, and from the Nomogen Formation at Haliut in the Erlian Basin, Nei Mongol, are probably contemporaneous, and both can be correlated approximately with the Gashato fauna of Mongolia (Zhou et al., 1976; Tong, 1978; Zhai et al., 1978). Tong (1978) also pointed out that the Taizicun fauna may be slightly older than the Gashato fauna and the Naran Bulak fauna, which may be the reason that Ting (1995, 1998) proposes to include this fauna in her Nongshanian Land Mammal Age. *Prodinoceras* dominates the fauna from the Taizicun Formation, whereas this genus has not been reported from the Nongshan Formation and its correlatives. Therefore, we cannot support a correlation between the Taizicun Formation and the Nongshan Formation and its correlatives.

Zhai (1978) described a coryphodont, *Coryphodon dabuensis*, and a uintathere, *Prodinoceras xinjiangensis* (= *Pyrodon xinjiangensis*), from the Dabu Formation in the Turfan Basin, and considered that *Coryphodon dabuensis* is morphologically close to North American Clarkforkian *C. proterus* and European *C. eocanus*. He also suggested the age of the Dabu Formation to be early Eocene, probably due to the widespread acceptance at that time of the Paleocene/Eocene boundary between the Tiffanian and Clarkforkian. In fact, he implied to correlate the Dabu fauna with the North American Clarkforkian (Zhai, personal communication). As mentioned above, the relationship between the Taizicun Formation and the Dabu Formation is not clear, but the uintathere fossil from the Dabu Formation seems to be more derived than those from the Taizicun Formation (Zhai, 1978). Therefore, we tentatively accept the Dabu Formation as a representative of a rock unit higher than the Taizicun Formation. *Prodinoceras xinjiangensis* has also been reported from the Nomogen Formation at Bayan Ulan (Meng et al., 1998). Both *Coryphodon* and *Prodinoceras* also occur in the Naran Member of the Naran Bulak Formation (Dashzeveg and Russell, 1988). In addition, Russell and Zhai (1987) considered that *Tienshanilophus* from the Taizicun Formation is probably referable to *Phenacolophus* from the Gashato of Mongolia. These records may indicate correlation of the Dabu Formation with the upper part of the Nomogen Formation and the Naran Member of the Naran Bulak Formation.

Although the uppermost beds in the Chijiang Basin, the Pinghu Formation, were originally considered to be younger than late Paleocene (Tong et al., 1979), the only mammal known from the formation, *Prodinoceras lacustris*, provides insufficient evidence for confident correlation. Russell and Zhai (1987) considered the Pinghu Formation to be equivalent to the strata bearing the Gashato fauna of Mongolia. According to Tong et al. (1976, 1979), the Pinghu Formation conformably overlies the Chijiang Formation. This, together with the occurrence of *Prodinoceras*, makes us think it reasonable to correlate the Pinghu Formation with the Nomogen and Taizicun/Dabu formations here.

The Shuangtasi Formation in the Xuancheng Basin, Anhui, has been considered to be either late Paleocene (Qiu et al., 1977; Li and Ting, 1983) or early Eocene (Zheng and Qiu, 1979; Zheng and Huang, 1986). The fossil mammals from the Shuangtasi Formation include only five species: *Wanotherium xuanchengensis*, the anagalid *Hsiuan-*

nania maguensis, the mesonychid *Dissacus magushanensis*, the arctostylopid *Bothriostylops progressus*, and the archaeolambdine *Archaeolambda yangtzeensis* (Tang and Yan, 1976; Xu, 1976; Yan and Tang, 1976; Huang, 1978; Zheng and Huang, 1986). These species appear to be more advanced than related forms from the Nongshan, Chijiang, and Doumu formations, but typical Eocene forms are unknown from the fauna. *Wanotherium* may not be useful for correlation because of its unique occurrence in the Xuancheng Basin, but the other four mammal taxa known from the Shuangtasi Formation are genera that mainly occur in Paleocene rocks of China. We suggest here that the fauna from the Shuangtasi Formation is younger than those from the Nongshan, Chijiang, and Doumu formations, but older than early Eocene faunas. It is most likely late Paleocene, probably correlative with faunas from the Taizicun and the Nomogen formations. The fact that *Dissacus magushanensis* is very close to ?*Dissacus* sp. (referred to *Dissacus serratus* by Meng et al., 1998) from the Nomogen Formation of Nei Mongol (Ting and Li, 1987) and *Palaeostylops iturus* has also been recovered from the Shuangtasi Formation (Huang Xueshi, personal communication) supports this correlation.

Huang and Chen (1997) reported the occurrence of three mammalian species in the Shuangtasi Formation in the Tongling Basin. Of these species, two, *Bothriostylops progressus* and *Archaeolambda* sp., cf. *A. yangtzeensis*, were also found in the Shuangtasi Formation in the Xuancheng Basin. This indicates that there is no notable difference between the age of the Shuangtasi Formation in both basins. In other words, the Shuangtasi Formation in both the Xuancheng and Tongling basins can be correlated with the Tazicun and Nomogen formations. Although the underlying Doumu Formation has not yet yielded fossil mammals, fossil charophytes resembling those from the type locality of the Doumu Formation in the Qianshan Basin (Chen, 1992) suggest a probable correlation of both of these Paleocene strata.

Another Paleocene rock unit, the Tujinshan Formation in the Jiashan Basin, Anhui, was recently reported to produce a mesonychid, *Sinonyx jiashanensis*, and some other fossil mammals (Zhou et al., 1995). Zhou et al. (1995:387) mentioned that "the middle and upper part of the Tujinshan Formation also yield *Sinostylops*, several kinds of anagalids, and a primitive eurymylid." Based on faunal comparisons, they considered that "the [fossil-bearing] beds are probably equivalent to the Doumu For-

mation of Qianshan County, Anhui" (Zhou et al., 1995:387). With the exception of *Sinonyx*, however, the fossil mammals from the Tujinshan Formation have yet to be described, and these identifictaions must be considered tentative. In addition, *Sinonyx* is much larger than a recently collected mesonychid from the Upper Member of the Doumu Formation. As such, the mammalian record from the Tujinshan Formation does not provide sufficient evidence to support a correlation of the Tujinshan Formation with the Doumu Formation. According to the Regional Geology of Anhui Province (Bureau of Geology and Mineral Resources of Anhui Province, 1985), the assemblages of ostracods and charophytes from the Tujinshan Formation also occur in the Shuangtasi and Pinghu formations. It therefore seems likely that the Tujinshan Formation correlates with the Shuangtasi Formation (and the Nomogen Formation and its correlatives) rather than with the Doumu Formation.

The lowest fossiliferous bed in the Lingcha Formation near Hengdong, Hunan, is possibly late Paleocene in age, because of the occurrence of *Archaeolambda* sp. 4. (Li et al., 1979, Wang, 1993).

Figure 5 summarizes our preferred correlation of the Chinese mammal-bearing Paleocene. If this correlation is broadly correct, we can determine the distribution of certain mammalian taxa in the Chinese Paleocene (Fig. 6): 1) Bemalambdidae and Astigalidae are restricted to the Shanghu Formation and correlative beds, from which the faunas define the Shanghuan Land Mammal Age (Li and Ting, 1983; Ting, 1995, 1998); 2) specimens of Pastoralodontidae and Arctostylopidae have never been recorded in faunas older than the Nongshanian Land Mammal Age (Li and Ting, 1983; Ting, 1995, 1998); 3) Paleocene Dinocerata have been reported only from the Nomogen Formation and its correlatives in China, faunas from which represent the Gashatan Land Mammal Age; 4) Anagalidae, Pseudictopidae, and Mesonychidae are present in virtually all Paleocene levels, with the exception that the Anagalidae are unknown from some Gashatan correlatives in North China, although they survived into the Oligocene in North China (Simpson, 1931; Bohlin, 1951).

One interesting issue is that there is some difference between the late Paleocene faunas from southern and northern China. For example, Glires are not rare in Paleocene basins north of the Yangtze River, but Glires have never been recorded from basins south of the Yangtze River. Paleocene multituberculates have only been recovered from late Paleocene strata in the Turfan and Erlian basins in China,

EPOCH	LMA	NAN-XIONG	CHI-JIANG	QIAN-SHAN	SANSHUI	CHALING	XINZHOU	SHIMEN	SHAN-YANG	XUAN-CHENG	TONG-LING	JIASHAN	TURFAN	ERLIAN	NORTH AMERICA
			CHINA												NORTH AMERICA
PALEOCENE	GASHATAN		PINGHU FM.							SHUANG-TASI FM.	SHUANG-TASI FM.	TUJIN-SHAN FM.	DABU FM. ? / TAIZI-CUN FM.	NOMO-GEN FM.	CLARK-FORKIAN
	NONGSHANIAN	NONGSHAN FM. / ZHUGUIKENG M. / DATANG M.	CHIJIANG FM. / LANNIKENG M. / WANGWU M.	DOUMU FM. / UPPER M. / LOWER M.							DOUMU FM. ?				TIFFANIAN
	SHANGHUAN	SHANG-HU FM.	SHIZI-KOU FM.	WANGHUDUN FM. / UPPER M. / MIDDLE M. / LOWER M.	FORMATION I OF BUXIN GROUP	ZAOSHI FM.	"DONGHU GROUP" ? ?	FANGOU FM. ?	JUAN-LING FM.						TORREJONIAN
															PUERCAN

Fig. 5.—Tentative correlation of Paleocene mammal-bearing rock units within China and with the North American sequence of land mammal "ages."

although they occur in the Early Cretaceous of Liaoning (Wang et al., 1995), the Late Cretaceous of Nei Mongol (Jerzykiewicz et al., 1993), and the early Eocene of Shandong (Tong and Wang, 1994).

These discrepancies in the taxonomic composition of late Paleocene mammalian faunas may result from paleoenvironmental differences between northern and southern China at that time.

SHANGHUAN	NONGSHANIAN	GASHATAN
Bemalambdidae		
Astigalidae		
	Pastoralodontidae	
	Arctostylopidae	
		Dinocerata
Anagalidae		
Pseudictopidae		
Mesonychidae		

Fig. 6.—Stratigraphic distribution of some major groups of Chinese Paleocene mammals. These taxa are useful for biostratigraphic correlation of Paleocene mammal-bearing rock units in China.

CORRELATION OF THE CHINESE MAMMAL-BEARING PALEOCENE WITH NORTH AMERICAN PALEOCENE LAND MAMMAL AGES

The general endemism of Chinese Paleocene mammal faunas, especially prior to the latest Paleocene, has been noted in several publications (e.g., South China "Red Beds" Research Group, 1977; Chow and Zheng, 1980; Archibald et al., 1987). Of the 27 mammalian families (undetermined families excluded) known from the Chinese Paleocene, 11 (40.7%) have also been recorded from the North American Paleocene. However, only two genera, *Dissacus* and *Coryphodon* (excluding the highly questionable Chinese record of *Ectoconus*), are known from strata of undoubted Paleocene age in both Asia and North America. In addition, two genera recorded in the late Paleocene Bayan Ulan local fauna of Nei Mongol, *Pachyaena* and *Prolimnocyon*, also occur in the early Wasatchian of North America (Meng et al., 1998), while *Alagomys* is known from the early Eocene (Bumbanian) of Shandong Province, China (Tong and Dawson, 1995), and Mongolia (Dashzeveg, 1990) and the Clarkforkian of North America (Dawson and Beard, 1996). No species of Paleocene mammal is known to have inhabited both Asia and North America. This considerable degree of endemism confounds attempts at accurate intercontinental correlation.

Early biostratigraphic studies of Chinese Paleocene mammals divided the known Paleocene mammalian faunas into two broad categories, presumably representing the early–middle and late Paleocene, respectively (South China "Red Beds" Research Group, 1977; Chow and Zheng, 1980). In particular, mammalian faunas known from the Shanghu, Shizikou, Zaoshi, Wanghudun, and Fangou formations were considered to represent the early–middle Paleocene, while those from the Nongshan, Chijiang, Doumu, Shuangtasi, Taizicun, and Nomogen formations were considered as late Paleocene (South China "Red Beds" Research Group, 1977; Zheng and Qiu, 1979; Chow and Zheng, 1980; Li and Ting, 1983; Russell and Zhai, 1987). Without providing formal definitions, Li and Ting (1983) proposed two Chinese provincial ages, the Shanghuan and the Nongshanian, to represent presumed correlation to early–middle and late Paleocene strata in Europe, respectively. Sloan (1987) favored Gashatan over Nongshanian, on the basis of priority of the former as a stage (age) name for the Asian late Paleocene. However, Tong et al. (1995) continued to divide the Chinese Paleocene

into two parts, using the Shanghuan and Nongshanian (the latter including some Gashatan correlatives) as early and late Paleocene provincial mammal ages of China.

In fact, the Gashato fauna is distinctly different from faunas derived from the Nongshan Formation and its correlatives in composition, and these compositional differences are almost certainly attributable to age. As such, we prefer to use both the Nongshanian and the Gashatan to distinguish Asian mammal faunas of different age, represented by the faunas from the Nongshan Formation and its correlatives and the faunas from the Gashato Formation and its correlatives, respectively. Chinese Paleocene mammal faunas that seem to be correlative with the Gashatan include those from the Pinghu, Shuangtasi, Taizicun, Dabu, and Nomogen formations. Ting (1995, 1998) also defined three land mammal ages, Shanghuan, Nongshanian, and Gashatan, and six interval zones for the Asian Paleocene on the basis of index fossils.

The Cretaceous/Paleocene boundary in China has been thoroughly studied only in the Nanxiong Basin, Guangdong. Based on interpretations of various types of paleontological data, many workers have argued that the contact between the Cretaceous Nanxiong Formation and the Paleocene Shanghu Formation is a disconformity, although there is no sedimentological evidence to support a discontinuity between these rock units (e.g., Zhou et al., 1977; Li and Ting, 1983; Chen, 1986; Russell and Zhai, 1987; Huang, 1988). In contrast, based on their studies of charophytes and ostracods, Huang (1979) and Zhang (1992) interpreted the contact between the Nanxiong and Shanghu formations as conformable. On the other hand, Mateer and Chen (1992) argued for an unconformity between the Late Cretaceous Nanxiong Formation and the Early Tertiary Shanghu Formation on the basis of conchostracans. Zhao et al. (1991) provided paleomagnetic results from the Nanxiong Formation (or Group) and the Shanghu Formation and interpreted the boundary between the Nanxiong and Shanghu formations as lying within the upper part of Chron 29r. These workers suggested that the Nanxiong/Shanghu boundary lies very close to the Cretaceous/Tertiary boundary, and provided further lithological criteria for distinguishing these formations in the field. They also considered that the contact between these

two formations is conformable. Based on this con-
clusion, Tong et al. (1995) suggested that the age
of the Shanghu Formation ranges from earliest Pa-
leocene through middle Paleocene. However, Rus-
sell et al. (1993) proposed an alternative interpre-
tation of the same paleomagnetic data. On the basis
of their attempts to reduce the sedimentation rate of
the upper part of the Nanxiong Formation (= the
Pingling Formation in Zhao et al. [1991] and Rus-
sell et al. [1993]), together with their understanding
of the mammal record and Li's (1989) pollen rec-
ord, Russell et al. (1993) recognized the interval of
reversed magnetic polarity around the Nanxiong/
Shanghu boundary as pertaining to two different in-
tervals, identified as chrons 31r and 26r, respective-
ly. However, the record of fossil mammals in the
Nanxiong Basin does not suggest that such a long
hiatus exists near the Cretaceous/Tertiary boundary
(see discussion below), although these data are in-
sufficient to establish whether or not the contact be-
tween the Shanghu and Nongshan formations is
conformable. The fossil mammal localities in the
Shanghu Formation range from the lower through
almost the uppermost part of this rock unit, rather
than being clustered near its base as Russell et al.
(1993) inaccurately claimed.

The Paleocene record of mammals in North
America is arguably the most nearly complete in the
world, and it has been relatively thoroughly studied.
Archibald et al. (1987) reviewed this record, rec-
ognizing four land mammal ages within the North
American Paleocene. Placement of the Paleocene/
Eocene boundary has varied: Rose (1981) suggested
it occurs within the Clarkforkian Land Mammal
Age, while others have argued that the Paleocene/
Eocene boundary lies at the Clarkforkian/Wasatch-
ian boundary (Hickey, 1980; Gingerich, 1989), or
within the early part of the Wasatchian Land Mam-
mal Age (e.g., Wing, 1984). Most recently, Wood-
burne and Swisher (1995), following Berggren et
al. (1995), placed the Paleocene/Eocene boundary
within the Wasatchian Land Mammal Age.

As noted previously, most Chinese Paleocene
mammals are endemic. Only a few genera are close-
ly related to North American Paleocene forms (Fig.
7). Based on these fossils, various attempts to cor-
relate the Chinese Paleocene with the North Amer-
ican Paleocene have been made (Li and Ting, 1983;
Sloan, 1987; Lucas and Williamson, 1995; Ting,
1995, 1998).

The first proposed correlation of the Shanghuan
with the North American sequence of Land Mam-
mal Ages was that of Zhou et al. (1977). They pro-

CHINA		NORTH AMERICA	
GASHATAN	*Coryphodon dabuensis*	CLARK-FORKIAN	*Alagomys* (Cf1) *Coryphodon proterus* (Cf1)
	Prodinoceras, Palaeostylops Tribosphenomys	TIFFANIAN	*Probathyopsis* (Ti5) *Arctostylops steini* (Ti5)
NONGSHANIAN	*Bothriostylops*		
	Asiostylops	TORREJONIAN	*Ictidopappus* (To3) *Dissacus navajovius* (To2)
SHANGHUAN	*Pappictidops Paranictops, Anictops Dissacus rotundus*		
	Dissacusium, Hukoutherium Yantanglestes conexus	PUERCAN	

Fig. 7.—Stratigraphic distribution of selected genera and species
of Paleocene mammals in China and North America and tentative
intercontinental correlation of Paleocene land mammal "ages"
in China and North America. *Paranictops* and *Anictops* are listed
here because they are closely related to taxa associated with the
unique radiometric date of 61.63 ± 0.92 Ma from the Xinzhou
Basin, Hubei Province.

posed that "the upper limit of the age of the Shan-
ghu fauna is probably not beyond the North Amer-
ican Torrejonian" and "at least the lower three fos-
siliferous beds are close to the Dragonian" which
was subsequently included in the Torrejonian Land
Mammal Age as its first interval zone by Archibald
et al. (1987). By the time the manuscript that Zhou
and his colleagues completed in 1973 was actually
published (Zhou et al., 1977), the authors had partly
revised their views on the age of the lower part of
the Shanghu Formation, stating that "the age
of...the Shanghu [Formation], especially its lower
zones, seems to be very close to the beginning of
Paleocene" (Zhou et al., 1977:100). Li and Ting
(1983), without discussion, tentatively correlated
the Shanghuan with the North American Puercan
and Torrejonian in their correlation chart. Sloan
(1987) correlated the Shanghuan with the Torrejon-
ian and part of the Tiffanian (To1 through Ti4),
based on his interpretation of mammalian evolution
and dispersal between Asia and North America.
Ting (1998) argued that "the Shanghuan is probably
partly or wholly correlative with the Torrejonian."
Lucas and Williamson (1995) proposed a correla-
tion of the Shanghuan with the North American
Puercan, based on their comparison of the evolu-
tionary stages of certain mammal taxa, including
Mesonychidae, Carnivora, Tillodontia, and Panto-
donta, and concluded that "there is no evidence the
Shanghuan mammals are younger than an early Pa-

leocene correlative of the North American Puercan" (Lucas and Williamson, 1995:104).

Among the few Paleocene mammal taxa shared between Asia and North America, mesonychids are relatively abundant, being represented in the Chinese Paleocene by some 11 species. *Dissacus rotundus* from the Zaoshi Formation, Hunan (correlative with the upper Shanghuan), seems close to North American *D. navajovius*, while *Yantanglestes conexus* from the Lower Member of the Wanghudun Formation (Qianshan Basin, Anhui) is thought to be the most primitive known mesonychid (Ting and Li, 1987). Both *Dissacusium* and *Hukoutherium* have dental features more primitive than those of North American *Dissacus* (Lucas and Williamson, 1995).

The carnivore *Pappictidops* from the lower part of the Upper Member of the Wanghudun Formation and the Upper Member of the Shanghu Formation appears close to North American *Ictidopappus* in dental structure (Qiu and Li, 1977; Wang, 1978). Lucas and Williamson (1995:102) argued that "*Pappictidops* is much more primitive than the Torrejonian carnivore *Protictis* in lacking a P^3 protocone and more resembles Torrejonian *Ictidopappus* but is more primitive in lacking a protocone on P^3 and lacking as well-developed a shearing ridge on the P^4." In fact, *Pappictidops* is similar and closely related to *Ictidopappus* (Qiu and Li, 1977; Wang, 1978), and *Protictis* may be in a different lineage from *Ictidopappus*, as Flynn and Galiano (1982) proposed. Some dental features of *Pappictidops*, such as its single-rooted P^1, expanded protocone on P^3, reduced posterior part of M^1, and reduced M^2 with respect to *Ictidopappus* (Qiu and Li, 1977), seemingly conflict with Lucas and Williamson's (1995) argument. Undescribed arctocyonid fossils from the lowest mammal-bearing bed of the Shanghu Formation appear to be close to mid-Puercan (Pu2) forms from North America (Luo Zhexi, personal communication). Therefore, fossils of Mesonychidae, Carnivora, and Arctocyonidae suggest a correlation of the Shanghuan with some part of both the North American Puercan and Torrejonian land mammal ages.

In addition to the mesonychids and carnivores discussed above, Lucas and Williamson (1995) compared tillodonts and pantodonts from the Nanxiong Basin and North America. Although Lucas and Williamson (1995:103) stressed "that *Deltatherium* is not a tillodont," they implied that "a *Deltatherium*-like form" could be a tillodont later in the same paper (Lucas and Williamson, 1995:105). These taxa are not useful for intercontinental correlation.

The pantodonts they compared are *Bemalambda* from China and *Pantolambda* from North America. In fact, the relationship between *Bemalambda* and *Pantolambda* is far from certain, although the former has been considered the most primitive pantodont (de Muizon and Marshall, 1992; Lucas, 1993). Zhao et al. (1991) and Xue et al. (1994, 1996) provided paleomagnetic results from the Nanxiong Basin and the Shanyang Basin, respectively. The results of Zhao et al. (1991) indicate that the Shanghuan spans the interval from latest Chron 29r through Chron 27r, while the results of Xue et al. (1994, 1996) show that *Bemalambda* occurs in Chron 27r. As such, both the mammalian and paleomagnetic records clearly suggest a correlation of the Shanghuan with the Puercan through mid-Torrejonian (Pu–To2) (Fig. 7), which is supported by the radiometric date measured from the basaltic sample in the Xinzhou Basin.

Uniquely in the Chinese Paleocene, intrusive basaltic rocks provide a minimum estimate of the age of strata yielding fossil mammals in the Xinzhou Basin. A K–Ar date of 61.63 ± 0.92 Ma was obtained from the basalt sample by Carl Swisher in 1989. Field observations suggest that the basaltic rocks must be younger than the upper fossiliferous bed in the Xinzhou Basin. This date falls late in Chron 27r according to the revised Geomagnetic Polarity Time Scale (Cande and Kent, 1992, 1995; Berggren et al., 1995). It also correlates with the *Tetraclaenodon/Pantolambda* Interval Zone (To2) of the Torrejonian Land Mammal Age in North America (Archibald et al., 1987; Prothero, 1995). Accordingly, the upper fossil-bearing bed in the Xinzhou Basin and its correlatives are no younger than mid-Torrejonian (To2).

As mentioned above, the Nongshanian *Bothriostylops* and *Sinostylops* are considered by Cifelli et al. (1989) to be more primitive than the Tiffanian (Ti5) *Arctostylops*. Based on this consideration, we provisionally suggest a correlation of the Nongshanian with the late Torrejonian through the late middle Tiffanian (To3–Ti4).

Other Paleocene mammal taxa known from both Asia and North America occur mainly in late Paleocene faunas. Of the several kinds of arctostylopids in Asia, only *Palaeostylops* and *Gashatostylops* are represented by abundant specimens. *Asiostylops* is considered to be the most primitive known arctostylopid genus (Zheng and Huang, 1986; Cifelli et al., 1989) and could be the sister group of the remaining taxa (Cifelli et al., 1989). Because of their retention of certain primitive characters, mem-

bers of the *Bothriostylops* + *Sinostylops* clade appear to lie outside a more advanced arctostylopid clade including *Palaeostylops, Gashatostylops, Arctostylops,* and two younger forms. Among these advanced genera, *Arctostylops* appears to be the most primitive (Cifelli et al., 1989). From the same strata that produce *Palaeostylops,* fossils of the dinoceratan *Prodinoceras* have also been collected. *Prodinoceras* is considered to be closely related to North American *Probathyopsis,* which first occurs in the late Tiffanian (Ti5). Both the arctostylopids and the dinoceratans of the Gashatan may indicate correlation of the lower part of the Gashatan with the upper part of the Tiffanian. Moreover, the occurrence of *Coryphodon tsaganensis* in the Naran Member of the Naran Bulak Formation in Mongolia and *C. dabuensis* in the Dabu Formation in the Turfan Basin suggests that the upper part of the Gashatan is correlative with the North American Clarkforkian. Here, we tentatively correlate the Gashatan with the late Tiffanian through Clarkforkian (Ti5–Cf). However, the occurrence of *Alagomys* in the overlying Bumban Member of the Naran Bulak Formation in Mongolia (Dashzeveg, 1990) and in the Wutu Formation in Shandong, China (Tong and Dawson, 1995), where *Alagomys* co-occurs with carpolestids (Beard and Wang, 1995), may conflict with correlation between the upper part of the Gash-

atan and the Clarkforkian. In North America, *Alagomys* is known only from the early Clarkforkian Big Multi Quarry in southwestern Wyoming (Dawson and Beard, 1996), while this genus is restricted to Bumbanian faunas in Asia. Obviously, more evidence is required to clarify intercontinental correlation of the Asian Paleocene.

Regarding the Paleocene/Eocene boundary in Asia, Dashzeveg (1988) placed it at the base of the Bumban Member of the Naran Bulak Formation (i.e., at the Gashatan/Bumbanian boundary) on the basis of the simultaneous appearance of perissodactyls, the primate *Altanius,* rodents, the condylarth *Hyopsodus,* and other taxa. He also correlated the upper limit of the Gashatan with the North American Clarkforkian/Wasatchian boundary. However, the stratigraphic occurrence of alagomyid rodents in Asia and North America raises doubts about this correlation, as noted previously. At this moment, the possibility of correlating the lower part of the Bumbanian with the Clarkforkian cannot be ruled out (Meng et al., 1998). Moreover, the Paleocene/Eocene boundary does not coincide with the Clarkforkian/Wasatchian boundary according to Woodburne and Swisher (1995). Further work is needed to clarify the position of the Paleocene/Eocene boundary in Asia, and resolution of this problem exceeds the scope of this paper.

CONCLUSIONS

In this paper, a brief introduction is provided to the lithostratigraphy and, insofar as possible, paleoenvironmental conditions characterizing Chinese Paleocene mammal-bearing basins. Recent advances in Chinese Paleocene paleomammalogy and biostratigraphy are summarized. On the basis of our current understanding of the fossil mammal record, we propose a revised correlation of the Chinese Paleocene. In this correlation, the boundary between the Shanghu and Nongshan formations in the Nanxiong Basin is correlated with the boundary between the Shizikou and Chijiang formations in the Chijiang Basin and with the middle part of the Upper Member of the Wanghudun Formation. In this case, the rock units considered to be correlative or partly correlative with the Shanghu Formation are the Shizikou, Zaoshi, Fangou, and Juanling formations and the Lower Member to the lower part of the Upper Member of the Wanghudun Formation, as well as the "Donghu Group" in the Xinzhou Basin. Correlatives of the Nongshan Formation include the

Chijiang Formation, the upper part of the Upper Member of the Wanghudun Formation, and the Doumu Formation. The Nomogen, Pinghu, Shuangtasi, Tujinshan, Taizicun, and Dabu formations are considered to be correlatives, all of which could be correlated with the Gashato Formation and the Naran Member of the Naran Bulak Formation in Mongolia.

Regarding intercontinental correlation between Asia and North America, the Shanghuan is correlated with the Puercan through the mid-Torrejonian (Pu–To2), while the Gashatan is tentatively correlated to the late Tiffanian through the Clarkforkian (Ti5–Cf). Accordingly, the Nongshanian is correlated with the late Torrejonian through the late middle Tiffanian (To3–Ti4). This intercontinental correlation is based on comparisons of some closely related mammal taxa in China and North America. Correlation of the Shanghuan/Nongshanian boundary with the North American Torrejonian (To2–To3) is also supported by paleomagnetic results and the

first radiometric date to be reported from Chinese Paleocene mammal-bearing rocks.

As noted previously, some aspects of our preferred correlation scheme require further corroboration, but this correlation hypothesis is the most reasonable one we can make at the present time. Certainly, further work will greatly improve our knowledge of Paleocene paleomammalogy and biostratigraphy in China.

ACKNOWLEDGMENTS

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APPENDIX

Mammalian Faunal Lists for Paleocene Basins in China

Only taxa that have been formally described are listed here; in some cases additional taxa are known but not yet published.

1. Nanxiong Basin, Guangdong (1 refers to the Shanghu Formation, 2 to the Nongshan Formation)
  Lipotyphla
    Family indet.
      Carnilestes palaeoasiaticus (Wang and Zhai, 1995) .... (1)
      C. major (Wang and Zhai, 1995) .... (1)

Anagalida
  Anagalidae
    Linnania lofoensis (Chow et al., 1973; Zhou et al., 1977) .... (1)
    cf. *Huaiyangale leura* (Ding and Tong, 1979) .... (2)
  Pseudictopidae
    Haltictops mirabilis (Ding and Tong, 1979) .... (2)
    H. meilingensis (Ding and Tong, 1979) .... (2)
  Astigalidae
    Astigale nanxiongensis (Zhang and Tong, 1981) .... (1)
    Zhujegale lirenensis (Zhang and Tong, 1981) .... (1)
    Z. jintangensis (Zhang and Tong, 1981) .... (1)
Tillodontia
  Esthonychidae
    Lofochaius brachyodus (Chow et al., 1973; Zhou et al., 1977) .... (1)
  Family indet.
    Interogale datangensis (Huang and Zheng, 1983; Ting and Zheng, 1989) ...... (2)
?Tillodontia
  Family indet.
    Dysnoetodon minuta (Zhang, 1980a) .... (1)
Mesonychia
  Mesonychidae
    Yantanglestes feiganensis (Chow et al., 1973; Zhou et al., 1977; Ideker and Yan, 1980) ...... (1)
    Y. datangensis (Wang, 1976; Ideker and Yan, 1980) .... (2)
    Dissacusium shanghoensis (Chow et al., 1973; Zhou et al., 1977) .... (1)
    Hukoutherium ambigum (Chow et al., 1973; Zhou et al., 1977) .... (1)
Condylarthra
  Hyopsodontidae
    Hyopsodontinae
      Yuodon protoselenoides (Chow et al., 1973; Zhou et al., 1977) .... (1)
    Mioclaeninae
      Palasiodon siurenensis (Chow et al., 1973; Zhou et al., 1977) .... (1)
  Periptychidae
    ?*Ectoconus* sp. (Zhou et al., 1977) .... (1)
  ?Phenacodontidae
    N. gen. and sp. (unnamed) (Zhou et al., 1977) .... (1)
Pantodonta
  Bemalambdidae
    Bemalambda nanhsiungensis (Chow et al., 1973; Zhou et al., 1977) .... (1)
    B. pachyoesteus (Chow et al., 1973; Zhou et al., 1977) .... (1)
    B. crassa (Chow et al., 1973; Zhou et al., 1977) .... (1)
  Pastoralodontidae
    Altilambda pactus (Chow and Wang, 1978) .... (2)
    A. sp. (Tong, 1982) .... (2)
  Pantolambdodontidae
    Archaeolambedinae
      Archaeolambda speciosa (Tong, 1978, 1982; Wang, 1993) .... (2)
      Nanlingilambda sp. (Tong, 1982) .... (2)
  New Family
    "*Altilambda*" *minor* (Tong, 1982; Wang, 1993) .... (2)
Carnivora
  Miacidae
    Pappictidops acies (Wang, 1978) .... (1)
    P. obtusus (Wang, 1978) .... (1)

Edentata
  Ernanodontidae
    Ernanodon antelios (Ding, 1979, 1987) .... (2)
?Primates
  Family indet.
      Petrolemur brevirostre (Tong, 1979*a*) .... (2)
Order indet.
  Phenacolophidae
    Minchenella grandis (Zhang, 1978, 1980*b*) .... (2)
    Yuelophus validus (Zhang, 1978) .... (2)
  ?Phenacolophidae
    Radinskya yupingae (McKenna et al., 1989) .... (2)

2. Sanshui Basin, Guangdong (Mammal fossil was collected from the Formation I of the Buxin Group)
Pantodonta
  Bemalambdidae
    ?*Hypsilolambda* sp. (Wang and Zhang, 1997)

3. Chijiang Basin, Jiangxi (1 refers to the Shizikou Formation, 2 to the Chijiang Formation, 3 to the Pinghu Formation)
Insectivora
  Didymoconidae
    Archaeoryctes notialis (Zheng, 1979*a*) .... (2)
Anagalida
  Anagalidae
    Hsiuannania minor (Ding and Zhang, 1979) .... (2)
  Pseudictopidae
    cf. *Pseudictops tenuis* (Ding and Tong, 1979; Ding and Zhang, 1979) .... (2)
Mesonychia
  Mesonychidae
    Jiangxia chaotoensis (Zhang et al., 1979) .... (2)
    ?*Dissacus* sp. (Zhang et al., 1979; Ting and Li, 1987) .... (2)
Condylarthra
  Hypsodontidae
    Gen. and sp. indet. (Zhang et al., 1979)
  Periptychidae
    ?Anisonchinae
      Pseudanisonchus antelios (Zhang et al., 1979) .... (2)
Pantodonta
  Bemalambdidae
    Bemalambda shizikouensis (Wang and Ding, 1979) .... (1)
    B. sp. (Wang and Ding, 1979) .... (1)
  Pantolambdodontidae
    Archaeolambdinae
      Archaeolambda tabiensis (Tong, 1979b; Wang, 1993) .... (2)
      A. sp. 1 (Tong, 1979*b*; Wang, 1993) .... (2)
      A. sp. 3 (Tong, 1979*b*; Wang, 1993) .... (2)
      Nanlingilambda chijiangensis (Tong, 1979*b*) .... (2)
  Harpyodidae
    Harpyodus decorus (Wang, 1979) .... (2)
Arctostylopida
  Arctostylopidae
    Asiostylops spanios (Zheng, 1979*b*) .... (2)
    Allostylops periconotus (Zheng, 1979*b*) .... (2)

    Bothriostylops notios (Zheng and Huang, 1986) .... (2)
    B. sp. (Zheng and Huang, 1986) .... (2)
Dinocerata
  Uintatheriidae
    Prodinoceras lacustris (Tong, 1979c; Schoch and Lucas, 1985) .... (3)
Order indet.
  Phenacolophidae
    Ganolophus lannikenensis (Zhang, 1979) .... (2)

4. Chaling Basin, Hunan (All fossils are from the Zaoshi Formation)
Anagalida
  ?Anagalidae
    Stenanagale xiangensis (Wang, 1975; Hu, 1993)
Mesonychia
  Mesonychidae
    Dissacus rotundus (Wang, 1975; Ting and Li, 1987)
Tillodontia
  Esthonychidae
    Meiostylodon zaoshiensis (Wang, 1975)
  Pantodonta
  Bemalambdidae
    Bemalambda nanhsiungensis (Chow et al., 1973; Wang, 1975)
    Hypsilolambda chalingensis (Wang, 1975)
    H. impensa (Wang, 1975)

5. Qianshan Basin, Anhui (1 refers to the Wanghudun Formation, 2 to the Doumu Formation)
Insectivora
  Didymoconidae
    Zeuctherium niteles (Tang and Yan, 1976) .... (1)
  Family indet.
    Hyracolestes ermineus (Matthew and Granger, 1925; Qiu and Li, 1977) .... (2)
Anagalida
  Anagalidae
    Eosigale gujingensis (Hu, 1993) .... (1)
    Huaiyangale chianshanensis (Xu, 1976) .... (1)
    Hsiuannania tabiensis (Xu, 1976) .... (2)
    H. sp. (Xu, 1976) .... (2)
    Qipania yui (Hu, 1993) .... (1)
  ?Anagalidae
    Diacronus wanghuensis (Xu, 1976; Hu, 1993) .... (1)
    Anaptogale wanghoensis (Xu, 1976; Hu, 1993) .... (1)
  Pseudictopidae
    Anictops tabiepedis (Qiu, 1977) .... (1)
    Paranictops majuscula (Qiu, 1977) .... (1)
    ?*P.* sp. (Qiu, 1977) .... (1)
    Allictops inserrata (Qiu, 1977) .... (2)
    Cartictops canina (Qiu and Li, 1977; Ding and Tong, 1979) .... (1)
  Astigalidae
    Astigale wanensis (Zhang and Tong, 1981) .... (1)
    Chianshania gianghuaiensis (Xu, 1976; Hu, 1993) .... (1)
  Family indet.
    Wanogale hodungensis (Xu, 1976; Hu, 1993) .... (1)
Mixodontia
  Eurymylidae
    Heomys orientalis (Li, 1977; Li et al., 1987) .... (2)

Mimotonia
  Mimotonidae
    Mimotona wana (Li, 1977; Li et al., 1987) .... (2)
    M. robusta (Li, 1977; Li et al., 1987) .... (2)
    M. lii (Dashzeveg and Russell, 1988) .... (1)
Carnivora
  Miacidae
    Pappictidops orientalis (Qiu and Li, 1977) .... (1)
Mesonychia
  Mesonychidae
    Yantanglestes conexus (Yan and Tang, 1976; Ideker and Yan, 1980) .... (1)
Pantodonta
  Bemalambdidae
    Bemalambda sp. (Huang, 1978) .... (1)
    Gen. and sp. indet. (Huang, 1978) .... (1)
  ?Alcidedorbignyidae
    N. gen. and sp. (Wang, 1993) .... (1)
  Harpyodidae
    Harpyodus euros (Qiu and Li, 1977; Wang, 1979) .... (1)
  Pastoralodontidae
    Altilambda pactus (Chow and Wang, 1978) .... (1)
    A. yujingensis (Wang et al., 1992) .... (1)
    A. tenuis (Chow and Wang, 1978) .... (1)
    A. n. sp. (Wang, 1993) .... (2)
Pantolambdodontidae
  Archaeolambdinae
    Archaeolambda tabiensis (Huang, 1977) .... (2)
  New Family
    N. gen. and sp. (Wang, 1993) .... (1)
Tillodontia
  Mesonychidae
    Plethorodon chienshanensis (Huang and Zheng, 1987; de Muizon and Marshall, 1992) .... (1)
Arctostylopida
  Arctostylopidae
    Sinostylops promissus (Tang and Yan, 1976) .... (2)
Order indet.
  Family indet.
    Decoredon anhuiensis (Xu, 1976, 1977; Szalay and Li, 1986) .... (1)
    Obtususdon hanhuaensis (Xu, 1977) .... (1, 2)
    Anchilestes impolitus (Qiu and Li, 1977) .... (1)
    Wania chowi (Wang, 1995; Nessov et al., 1998) .... (1)

6. Xuancheng Basin, Anhui (All fossils are from the Shuangtasi Formation)
Anagalida
  Anagalidae
    Hsiuannania maguensis (Xu, 1976)
Mesonychia
  Mesonychidae
    Dissacus magushanensis (Yan and Tang, 1976)
Arctostylopida
  Arctostylopidae
    Bothriostylops progressus (Tang and Yan, 1976; Zheng and Huang, 1986)

Pantodonta
  Pantolambdodontidae
    Archaeolambdinae
      Archaeolambda yangtzeensis (Huang, 1978)
Order indet.
  Family indet.
    Wanotherium xuanchengensis (Tang and Yan, 1976)

7. Tongling Basin, Anhui (All fossils are from the Shuangtasi Formation)
Arctostylopida
  Arctostylopidae
    Bothriostylops progressus (Tang and Yan, 1976; Zheng and Huang, 1986; Huang and Chen, 1997)
Pantodonta
  Pantolambdodontidae
    Archaeolambda sp. cf. *A. yangtzeensis* (Huang, 1978; Huang and Chen, 1997)
    Guichilambda zhaii (Huang and Chen, 1997)

8. Jiashan Basin, Anhui (The fossil is from the Tujinshan Formation)
Mesonychia
  Mesonychidae
    Sinonyx jiashanensis (Zhou et al., 1995)

9. Shimen Basin, Shaanxi (All fossils are from the Fangou Formation)
Insectivora
  Family indet.
    Prosarcodon luonanensis (McKenna et al., 1984)
Anagalida
  Anagalidae
    Linnania qinlingensis (Xue, 1986)
Pantodonta
  Bemalambdidae
    Bemalambda zhoui (Xue et al., 1996)
    B. sp. cf. *B. pachyoesteus* (Chow et al., 1973; Xue et al., 1996)
Mesonychia
  Mesonychidae
    Hukoutherium shimenensis (Qi and Huang, 1982)

10. Shanyang Basin, Shaanxi (The fossil is from the Juanling Formation)
Pantodonta
  Bemalambdidae
    Bemalambda sp. cf. *B. pachyoesteus* (Chow et al., 1973; Xue et al., 1996)

11. Turfan Basin, Xinjiang (1 refers to the Taizicun Formation, 2 to the Dabu Formation)
Multituberculata
  Fam., gen., and sp. indet. (Tong, 1978) . . . . (1)
Mixodontia
  Eurymylidae
    Gen. and sp. indet. (Tong, 1978) . . . . (1)
Anagalida
  Pseudictopidae
    Pseudictops chaii (Tong, 1978) . . . . (1)
Pantodonta
  Pantolambdodontidae
    Archaeolambdinae
      Archaeolambda speciosa (Tong, 1978; Lucas, 1982) . . . . (1)
      A. sp. 2 (Tong, 1978; Wang, 1993) . . . . (1)
  Coryphodontidae
    Coryphodon dabuensis (Zhai, 1978) . . . . (2)

Dinocerata
  Uintatheriidae
    Prodinoceras turfanensis (Chow, 1960; Tong, 1978; Schoch and Lucas, 1985) .... (1)
    P. diconicus (Tong, 1978; Schoch and Lucas, 1985) .... (1)
    P. primigenum (Tong, 1978; Schoch and Lucas, 1985) .... (1)
    P. simplum (Tong, 1978; Schoch and Lucas, 1985) .... (1)
    P. xinjiangensis (Zhai, 1978; Schoch and Lucas, 1985) .... (2)
Order indet.
  Phenacolophidae
    Tienshanilophus subashiensis (Tong, 1978) .... (1)
    T. lianmuqinensis (Tong, 1978) .... (1)
    T. shengjinkouensis (Tong, 1978) .... (1)

12. Erlian Basin, Nei Mongol (All fossils are from the Nomogen Formation)

Multituberculata
  Lambdopsalidae
    Lambdopsalis bulla (Chow and Qi, 1978)
  Taeniolabididae
    Prionessus lucifer (Matthew and Granger, 1925; Chow and Qi, 1978)
    Sphenopsalis nobilis (Matthew et al., 1928; Chow and Qi, 1978)
Lipotyphla
  Soricomorpha
    Nyctitheriidae
      Bayanulanius tenuis (Meng et al., 1998)
Insectivora
  Family indet.
    Sarcodon minor (Meng et al., 1998)
    S. pygmaeus (Matthew and Granger, 1925; Chow and Qi, 1978)
    Hyracolestes ermineus (Matthew and Granger, 1925; Chow and Qi, 1978)
  Palaeoryctoidea
    Gen. and sp. indet. (Meng et al., 1998)
  ?Leptictidae
    N. gen. and sp. (unnamed) (Meng et al., 1998)
Anagalida
  Pseudictopidae
    Pseudictops lophiodon (Matthew et al., 1929; Chow and Qi, 1978)
Creodonta
  Hyaenodontidae
    Limnocyoninae
      Prolimnocyon chowi (Meng et al., 1998)
?Creodonta
  Family indet.
    Gen. and sp. indet. (Meng et al., 1998)
Mixodontia
  Eurymylidae
    Eomylus borealis (Chow and Qi, 1978; Dashzeveg and Russell, 1988)
    ?Khaychina elongata (Dashzeveg and Russell, 1988; Meng et al., 1998)
Rodentia
  Alagomyidae
    Tribosphenomys minutus (Meng et al., 1994)
Arctostylopida
  Arctostylopidae
    Palaeostylops iturus (Matthew and Granger, 1925; Chow and Qi, 1978)
    Gashatostylops macrodon (Matthew and Granger, 1925; Chow and Qi, 1978; Cifelli et al., 1989)

Pantodonta
  Pastoralodontidae
    Pastoralodon lacustris (Chow and Qi, 1978)
    P. haliutensis (Chow and Qi, 1978; Wang, 1993)
    Convallisodon convexus (Chow and Qi, 1978)
Dinocerata
  Uintatheriidae
    Prodinoceras xinjiangensis (Zhai, 1978; Schoch and Lucas, 1985; Meng et al., 1998)
Mesonychia
  Mesonychidae
    Pachyaena sp. (Meng et al., 1998)
    Dissacus serratus (Chow and Qi, 1978; Meng et al., 1998)
Perissodactyla
  Family indet.
    Gen. and sp. indet. (Meng et al., 1998)

PALEOCENE AND EARLY EOCENE LAND MAMMAL AGES OF ASIA

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ABSTRACT

This paper attempts to define Asian Paleocene (Shanghuan, Nongshanian, and Gashatan) and early Eocene (Bumbanian) land mammal ages and zones. New correlations between these Asian land mammal ages and the better known biostratigraphic sequences of North America and Europe are proposed in light of recent paleontological discoveries in China and Mongolia.

The Shanghuan Land Mammal Age, subdivided into the *Bemalambda* Interval Zone and the *Archaeolambda* Interval Zone, may correlate to the Torrejonian of North America. The Nongshanian Land Mammal Age, which includes the *Asiostylops* Interval Zone and the *Sinostylops* Interval Zone, is considered correlative to the Tiffanian of North America. The Gashatan Land Mammal Age is correlative to the Clarkforkian of North America. The Bumbanian Land Mammal Age, including the *Orientolophus*, *Homogalax*, and *Heptodon* interval zones, is correlated to the North American Wasatchian.

Asian Paleocene mammal faunas contain mainly endemic taxa. Asian early Eocene faunas are much less endemic, reflecting major faunal exchange between Asia and North America.

INTRODUCTION

Asian Cenozoic mammals are virtually restricted to continental rocks, and most of these mammal-bearing strata are unconstrained radioisotopically. As such, fossil mammals have become the primary tool for biostratigraphic correlation and subdivision of Asian Cenozoic strata.

In the 1960s, Romer (1966) erected a series of Asian land mammal ages. Over the past two decades numerous discoveries of Paleocene and early Eocene fossil mammals in China and Mongolia have added tremendously to our understanding of early mammal evolution in Asia. Using these new data, Li and Ting (1983), Savage and Russell (1983), Russell and Zhai (1987), Sloan (1987), and Dashzeveg (1988) proposed correlations for the Asian faunas.

Li and Ting (1983) suggested tentative "Chinese Provincial Ages" based on mammals in their correlation table. Russell and Zhai (1987) named several Asian land mammal ages. Both of these publications are mainly summaries, and neither of them provide formal definitions and descriptions of Asian land mammal ages. The names of the Asian Paleocene and early Eocene land mammal ages used here—Shanghuan, Nongshanian, Gashatan, and Bumbanian—have been proposed by previous au-

thors (Romer, 1966; Szalay and McKenna, 1971; Li and Ting, 1983; Russell and Zhai, 1987). In this paper I attempt to define these Asian land mammal ages and to establish mammal zones with reference to the International Stratigraphic Guide (ISG; Hedberg, 1976) and the North American Stratigraphic Code (NASC; North American Commission on Stratigraphic Nomenclature, 1983), thereby providing a more secure basis for worldwide correlation.

I define Asian Paleocene and early Eocene mammal zones as interval zones (NASC, 1983:862). The zones are named for first-appearing species within each interval, so that each zone reflects a distinctive evolutionary event in the history of early Asian mammals. Two zones, the *Bemalambda* Interval Zone and the *Archaeolambda* Interval Zone, are recognized in the Shanghuan. The *Asiostylops* Interval Zone and the *Sinostylops* Interval Zone are recognized in the Nongshanian. The Taizicun fauna of the Turfan Basin in Xinjiang may represent a third zone in the Nongshanian. The Gashato, Naran, and Bayan Ulan faunas probably represent a mammal zone in the Gashatan. However, the temporal relationships among the Taizicun fauna and the Gashatan faunas require further study. No formal zones are erected for them at present. The Bumban-

ian is subdivided into the *Orientolophus* Interval Zone, the *Homogalax* Interval Zone, and the *Heptodon* Interval Zone.

My analysis of Paleocene and early Eocene Asian mammals for this study has depended heavily on available publications, some of the earlier of which are very brief. However, detailed study of all relevant specimens is beyond the scope of this paper. Thus, revisions and corrections are both expected and welcome as the specimen base expands and as systematic research on early Paleogene Asian mammals continues.

ASIAN PALEOCENE LAND MAMMAL AGES

Asian Paleocene strata can be assigned to one of three broad intervals on the basis of fossil mammals. The oldest of these is well represented in central and southern China, and includes the Shanghu Formation, Nanxiong Basin, Guangdong Province; the Shizikou Formation, Chijiang Basin, Jiangxi Province; the Zaoshi Formation, Chaling Basin, Hunan Province; the Wanghudun Formation, Qianshan Basin, Anhui Province; the Gaoyugou Formation, Tantou Basin, Henan Province; and the Fangou Formation, Shimen Basin, Shaanxi Province. Strata belonging to the intermediate Paleocene interval are distributed in both northern and southern China, and include the Nongshan Formation, Nanxiong Basin, Guangdong Province; the Chijiang Formation, Chijiang Basin, Jiangxi Province; the Doumu Formation, Qianshan Basin, Anhui Province; the Dazhang Formation, Tantou Basin, Henan Province; and the Taizicun Formation, Turfan Basin, Xinjiang Uygur Autonomous Region. The youngest Paleocene interval is represented in both Mongolia and China, and includes the Gashato (= Khashat) Formation, Ulan Nur Basin, the Naran and Zhigden members of the Naran Bulak Formation, Nemegt Basin, and the Naran Formation, Bugintsav Basin, all in Mongolia; and the Bayan Ulan and Nomogen formations of the Nomogen (Naomugen) area, Inner Mongolia (Nei Mongol Autonomous Region), and the Shuangtasi Formation, Xuancheng Basin, Anhui Province, in China (Fig. 1).

SHANGHUAN LAND MAMMAL AGE

The establishment of the Shanghuan Land Mammal Age is largely based on work in the Nanxiong Basin, Guangdong Province, China (Young and Chow, 1962). The term "Shanghu" is derived from the name of a small village, "Shanghudong," in that basin. Zhou et al. (1977:89) first used the term "Shanghu" for the "Middle" Paleocene strata, or "Shanghu Member" of the "Lofozhai Formation" (Chang and Tung, 1963; Cheng et al., 1973; Chow et al., 1973b), where the fossil mammals were found in the Nanxiong Basin. Tong et al. (1976:17) ele-

vated the "Shanghu Member" to formational status. Li and Ting (1983) suggested the term "Shanghuan" to represent a tentative "Chinese Provincial Age" in their correlation table, in which the "Shanghuan" straddled the line between "Early and Middle Paleocene." I advocate continued use of the term "Shanghuan" for the first Asian land mammal age of the Cenozoic Era, the Shanghuan Land Mammal Age. The beginning of the Shanghuan is recognized by the appearance of the orders Pantodonta, Anagalida, and Acreodi.

Definition and Characterization

The Shanghuan Land Mammal Age is defined here to include the time between the first appearance of the order Pantodonta, represented by *Bemalambda*, and the first appearance of the order Arctostylopida, represented by *Asiostylops*. Several mammalian orders, including Pantodonta, Anagalida, Carnivora, Acreodi, Tillodontia, and Condylarthra, and families, including Didymoconidae, Eurymylidae, Mimotonidae, and possibly Omomyidae (*Decoredon*), made their first appearance during this interval. The pantodont family Bemalambdidae disappeared during this interval.

Zonation

Two interval zones are recognized within the Shanghuan Land Mammal Age: the *Bemalambda* Interval Zone and the *Archaeolambda* Interval Zone (Fig. 2).

Bemalambda *Interval Zone.*—This zone is defined to include faunas occurring during the time between the first appearance of *Bemalambda* and the first appearance of *Archaeolambda*. It is characterized as follows:

First appearance of: Bemalambdidae, represented by *Bemalambda nanhsiungensis* and *B. pachyoesteus* (Zhou et al., 1977); Anagalidae, represented by *Wanogale hodungensis*, *Chianshania gianghuaiensis*, *Anaptogale wanghoensis*, and *Linnania lofoensis*; Pseudictopidae, represented by *Cartictops canina*, *Anictops tabiepedis*, and *Paranictops* sp. (Xu,
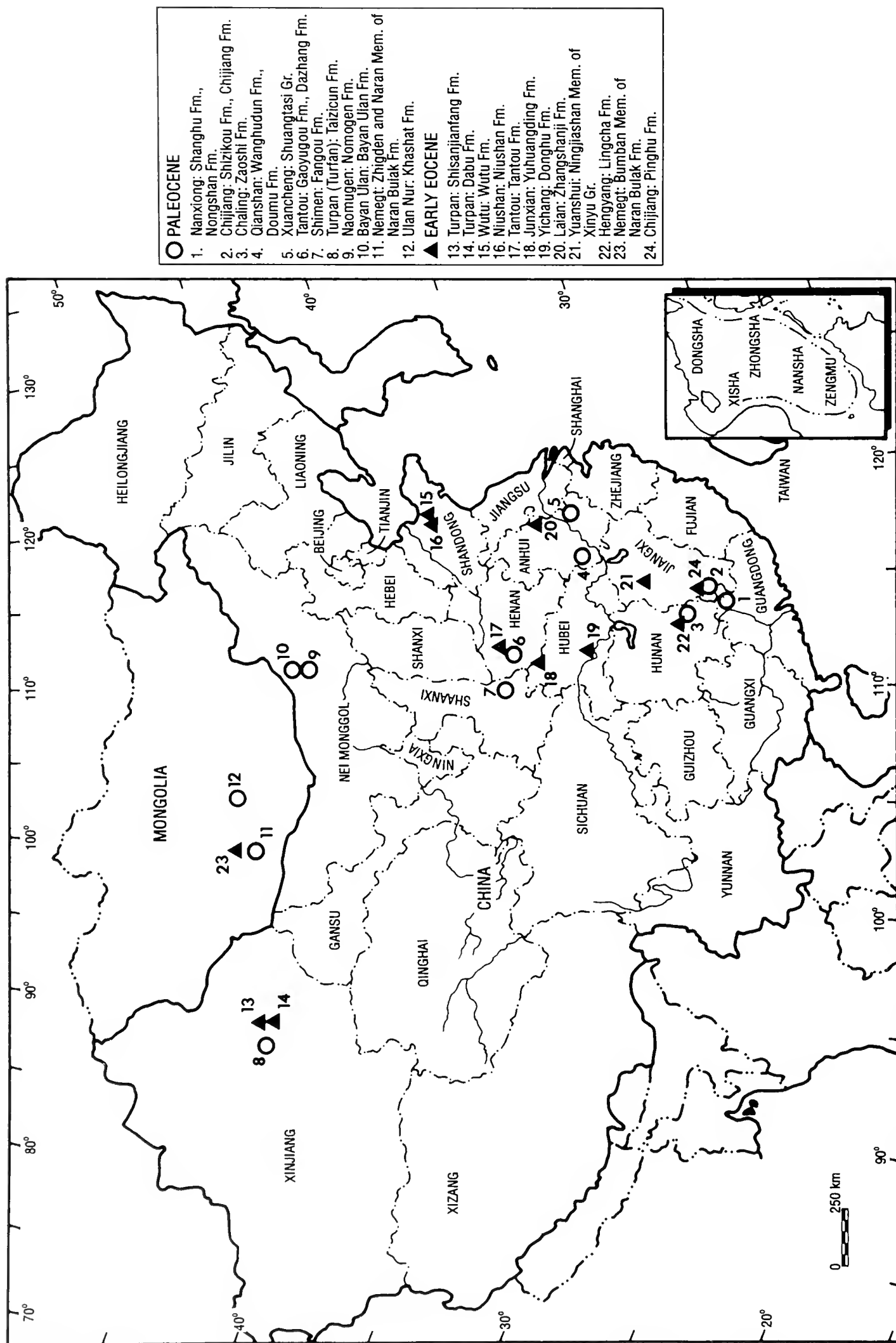
○ PALEOCENE

1. Nanxiong: Shanghu Fm.,
   Nongshan Fm.
2. Chijiang: Shizikou Fm., Chijiang Fm.
3. Chaling: Zaoshi Fm.
4. Qianshan: Wanghudun Fm.,
   Doumu Fm.
5. Xuancheng: Shuangtasi Gr.
6. Tantou: Gaoyugou Fm., Dazhang Fm.
7. Shimen: Fangou Fm.
8. Turpan (Turfan): Taizicun Fm.
9. Naomugen: Nomogen Fm.
10. Bayan Ulan: Bayan Ulan Fm.
11. Nemegt: Zhigden and Naran Mem. of
    Naran Bulak Fm.
12. Ulan Nur: Khashat Fm.

▲ EARLY EOCENE

13. Turpan: Shisanjianfang Fm.
14. Turpan: Dabu Fm.
15. Wutu: Wutu Fm.
16. Niushan: Niushan Fm.
17. Tantou: Tantou Fm.
18. Junxian: Yuhuangding Fm.
19. Yichang: Donghu Fm.
20. Laian: Zhangshanji Fm.
21. Yuanshui: Ningjiashan Mem. of
    Xinyu Gr.
22. Hengyang: Lingcha Fm.
23. Nemegt: Bumban Mem. of
    Naran Bulak Fm.
24. Chijiang: Pinghu Fm.

Fig. 1.—Geographic distribution of Paleocene and early Eocene fossil mammal localities in eastern Asia.

Age	Land Mammal Age	Zonation	First appearance of taxa		Rock Units	
			Representative	Auxiliary	Representative	Included
Early Eocene	Bumbanian	Heptodon Interval Zone	Heptodon tienshanensis	Advenimus hupeiensis	Shisanjianfang Fm.	Niushan Fm., Yuhuangding Fm. Zhangshanji Fm., Ningjiashan mem. of Xinyu Gr.
	Bumbanian	Homogalax Interval Zone	Homogalax wutuensis	Chronolestes simul	Wutu Fm.	?Aguyt mem.of Naran Bulak Fm. Mem. III of Khashat Fm.
	Bumbanian	Orientolophus Interval Zone	Orientolophus hengdongensis	Cocomys lingchaensis	Bumban mem. of Naran Bulak Fm. Lingcha Fm.	Dabu Fm., ?Pinghu Fm. Mem. II of Khashat Fm.
Paleocene L.	Gashatan	Gashatan Faunas	Tribosphenomys minutus	Coryphodon tsaganensis	mem. I of Khashat Fm. Naran mem. of Naran Bulak Fm. Bayan Ulan Fm.	?Shuangtasi Fm. ?Nomogen Fm. Zhigden mem. of Naran Bulak Fm.
	Nongshanian	?Taizicun Fauna	Prodinoceras diconicus	Multituberculata indet.	Taizicun Fm.	
	Nongshanian	Sinostylops Interval Zone	Sinostylops promissus	Ernanodon antelios	Upper mem. of Doumu Fm.	Datang mem. of Nongshan Fm. Wangwu mem. of Chijiang Fm.
	Nongshanian	Asiostylops Interval Zone	Asiostylops spanios	Ganolophus lanikenensis	Lannikeng mem. of Chijiang Fm.	Zhuguikeng mem. of Nongshan Fm. Lower mem. of Doumu Fm., ?Dazhang Fm.
	Shanghuan	Archaeolambda Interval Zone	Archaeolambda sp. n.	Heomys sp. Mimotona wana	upper part of Shanghu Fm.	Upper mem. of Wanghudun Fm. Shizikou Fm., Zaoshi Fm., Gaoyugou Fm.
Paleocene E.	Shanghuan	Bemalambda Interval Zone	Bemalambda nanhsiungensis	Yantanglestes conexus	lower part of Shanghu Fm.	Lower mem. of Wanghudun Fm. lower part of Fangou Fm.

Fig. 2.—Biostratigraphic zonation of the Shanguan–Bumbanian land mammal ages of Asia.

1976a, 1976b; Qiu, 1977); and Mesonychidae, represented by *Yantanglestes conexus, Y. feiganensis, Dissacusium shanghoensis,* and *Hukoutherium ambiguum* (Yan and Tang, 1976; Zhou et al. 1977). *Yantanglestes conexus* is the most primitive known mesonychid.

Characteristic fossils: *Bemalambda nanhsiungensis, Yantanglestes,* and *Hukoutherium.*

The *Bemalambda* Interval Zone is best represented by faunas from the lower part (or lower three fossil layers of Zhou et al., 1977) of the Shanghu Formation, Nanxiong Basin, Guangdong Province; the Lower Member of the Wanghudun Formation (Qiu et al., 1977), Qianshan Basin, Anhui Province; and the lower part of the Fangou Formation (McKenna et al., 1984), Shimen Basin, Shaanxi Province.

Zhou et al. (1977) recognized four mammal-bearing beds (zones) of the "Shanghu Member" of the "Lofochai Formation": the lower (maximum thickness 281 m), the middle (maximum 320 m), the upper (maximum 234 m), and the uppermost (thickness uncertain). The taxa in the lower unit include *Bemalambda nanhsiungensis, B. pachyoesteus, Yuodon protoselenoides, Palasiodon siurenensis,* and *Dissacusium shanghoensis;* in the middle, *B. nanhsiungensis, B. pachyoesteus, Linnania lofoensis, Yantanglestes feiganensis, Hukoutherium ambigum,* and *?Ectoconus* sp.; in the upper, *B. nanhsiungensis;* and in the uppermost, *B. crassa* and *Lofochaius brachyodon.* The lower, middle, and upper beds belong to the *Bemalambda* Interval Zone zone. The uppermost bed will be discussed in the following section. Zhou et al. (1977:88) suggested that the Shanghu fauna "can well be correlated with one of the Torrejonian stages" and "especially its lower zone, may range down to the beginning of the Middle Paleocene, or even earlier."

Qiu et al. (1977) subdivided the Wanghudun Formation into Lower (maximum thickness about 1000 m) and Upper members. No fossils have been found in the interval about 300 m thick between the Lower and Upper members. The Lower Member belongs to the *Bemalambda* Interval Zone; the Upper Member will be discussed in the following section. Taxa from the Lower Member include *Anchilestes impolitus, Wanogale hodungensis, Anaptogale wanghoensis, Chianshania gianghuaiensis, Cartictops canina, Anictops tabiepedis, Yantanglestes conexus, Plethorodon chienshanensis, Astigale wanensis, Paranictops* sp., and *Bemalambda* sp. (Xu, 1976a, 1976b; Yan and Tang, 1976; Qiu and Li, 1977; Zhang and Tong, 1981; Huang and Zheng, 1987).

Qiu et al. (1977:88) suggested that the Wanghudun Formation is "middle Paleocene," and that the fauna from the Lower Member differs from that of the Upper and might be "early Paleocene."

McKenna et al. (1984) recognized two fossil-bearing beds from the Fangou Formation. Four taxa, *Linnania qinglingensis, Prosarcodon lonanensis, Hukoutherium shimenensis,* and *Bemalambda,* are found in the lower of the two fossiliferous units in the Fangou Formation. *Prosarcodon lonanensis* is the most primitive species of palaeoryctoid insectivore known from Asia. This fauna is tentatively assigned to the *Bemalambda* Interval Zone.

Archaeolambda *Interval Zone.*—This zone is defined to include faunas occurring during the time between the first appearance of *Archaeolambda* and the first appearance of *Asiostylops.* It is characterized as follows:

First appearance of: Archaeolambdidae, represented by a new species of *Archaeolambda* (Ting et al., in press); Eurymylidae, the nearest relatives of rodents, represented by *Heomys* sp. (Li, 1977); Mimotonidae, the nearest relatives of lagomorphs, represented by *Mimotona wana* (Li, 1977); Miacidae, represented by *Pappictidops orientalis, P. acies,* and *P. obtusus* (Qiu and Li, 1977; Wang, 1978); Didymoconidae, represented by *Zeuctherium niteles* (Tang and Yan, 1976); and "the oldest recognized member of the primate semiorder Euprimates" (Szalay and Li, 1986:387), *Decoredon anhuiensis.*

Last occurrence of Bemalambdidae.

Characteristic fossils: *Bemalambda shizikouensis, B. crassa, Archaeolambda* n. sp., *Pappictidops,* and *Huaiyangale.*

The *Archaeolambda* Interval Zone is best represented by faunas from the upper part (uppermost bed of Zhou et al., 1977) of the Shanghu Formation, Nanxiong Basin, Guangdong Province; and the Upper Member of the Wanghudun Formation, Qianshan Basin, Anhui Province. Also assigned to the *Archaeolambda* Interval Zone zone are faunas from the Shizikou Formation, Chijiang Basin, Jiangxi Province; the Zaoshi Formation, Chaling Basin, Hunan Province; and the Gaoyugou Formation, Tantou Basin, Henan Province.

The upper part of the Shanghu Formation yields the earliest known species of *Archaeolambda, Bemalambda crassa* and *Lofochaius brachyodon.* Zhou et al. (1977:7) proposed that the "uppermost fossil zone" is "apparently distinct from the others and may represent a fauna zone or even a fauna of younger age." *Archaeolambda* is a common genus

in the Nongshanian, which has not been previously shown to occur in the Shanghuan. A new species of *Archaeolambda* recently recovered from the uppermost bed of the "Shanghu Member" (Ting et al., in press) not only demonstrates the existence of archaeolambdids in the Shanghuan, but also further supports the suggestion of Zhou et al. (1977) that the fauna in the uppermost bed may be recognized as pertaining to another zone, which is here named the *Archaeolambda* Interval Zone.

The Upper Member (500 m thick) of the Wanghudun Formation is the major fossil-bearing unit in the Qianshan Basin. The taxa known from these strata include *Eosigale gujingensis, Qipania yui, Huaiyangale chianshanensis, Diacronus wanghuensis, Heomys* sp., *Mimotona wana, Anictops tabiepedis, Paranictops majuscula, Pappictidops orientalis, Decoredon anhuiensis, Altilambda pactus, A. tenuis, Harpyodus euros, Zeuctherium niteles,* and *Obtususdon hanhuaensis* (Tang and Yan, 1976; Wang, 1976, 1979; Li, 1977; Qiu, 1977; Szalay and Li, 1986; Hu, 1993). Qiu et al. (1977) suggested that the fauna from the Upper Member of the Wanghudun Formation is "middle Paleocene."

Two taxa are known from the Shizikou Formation, *Bemalambda shizikouensis* and *Archaeolambda.* The Shizikou faunal composition is similar to that of the upper part of the Shanghu Formation, and they are probably coeval (Tong et al., 1979).

Six taxa are known from the Zaoshi Formation (53 m thick): *Stenanagale xiangensis, Dissacus rotundus, Meiostylodon zaoshiensis, Bemalambda nanhsiungensis, Hypsilolambda chalingensis,* and *H. impensa* (Wang, 1975). This fauna is characterized by diversified pantodonts, *Hypsilolambda,* and an advanced mesonychid, *Dissacus rotundus.* Gao (1975) suggested that the Zaoshi fauna is "late middle Paleocene" and comparable to the fauna from the Upper Member of the Wanghudun Formation.

Mammals from the upper part of the Fangou Formation (McKenna et al., 1984) and the Gaoyugou Formation have not been published. I tentatively assign them to the *Archaeolambda* Interval Zone based on their relative stratigraphic position.

NONGSHANIAN LAND MAMMAL AGE

Establishment of the Nongshanian Land Mammal Age is mainly based on work in the Nanxiong Basin, Guangdong Province, and the Chijiang Basin, Jiangxi Province, China. "Nongshan" is the name of a small hill in the Nanxiong Basin. This term was first used by Zhou et al. (1977) to name a stratigraphic unit, the "Nongshan Member," overlying

the "Shanghu Member" of the "Lofochai Formation." Zhou et al. (1977) considered the Nongshan Member to be "?late Paleocene" in age. Tong et al. (1976) proposed "Nongshan Formation" for the same strata. Li and Ting (1983) proposed the term "Nongshanian" for their tentative late Paleocene "Chinese Provincial Age." However, Sloan (1987) advocated continued use of the earlier term "Gashatan" (Romer, 1966) for the late Paleocene Asian mammal age. Here, both the "Nongshanian" and "Gashatan" are recognized as valid and successive Asian land mammal ages. The beginning of the Nongshanian is marked by the appearance of the order Arctostylopida.

Definition and Characterization

The Nongshanian Land Mammal Age is defined here to include the time between the first appearance of the order Arctostylopida, represented by *Asiostylops,* and the first appearance of the order Rodentia, represented by *Tribosphenomys.* The orders Arctostylopida and Dinocerata and the families Phenacolophidae and Ernanodontidae made their first appearances during this interval. In addition, Multituberculata appear for the first time in the Cenozoic of Asia during the Nongshanian. Archaeolambdids, including at least four species of *Archaeolambda* (Tong, 1979a), are very common and diverse during this interval. Phenacolophids include seven species of four genera, *Ganolophus, Minchenella, Tienshanilophus,* and *Yuelophus* (Tong, 1978; Zhang, 1978, 1979). Nongshanian Multituberculata and Dinocerata are known from Mongolia and northern China, but these taxa did not occur in southern China at that time.

Zonation

Two interval zones are recognized within the Nongshanian Land Mammal Age: the *Asiostylops* Interval Zone and the *Sinostylops* Interval Zone (Fig. 2). In addition, the fauna from the Taizicun Formation, Turfan Basin, Xinjiang Uygur Autonomous Region, is tentatively assigned to the Nongshanian Land Mammal Age, but the biostratigraphic relationships of this fauna require further study.

Asiostylops *Interval Zone.*—This zone is defined to include faunas occurring during the time between the first appearance of *Asiostylops* and the first appearance of *Sinostylops.* It is characterized as follows:

First appearance of: Arctostylopidae, represented by the most primitive species *Asiostylops spanios* (Zheng, 1979); Phenacolophidae, represented by

Ganolophus lanikenensis (Zhang, 1979); the anagalids *Hsiuannania tabiensis* and *H. minor*; and the pseudictopids *Allictops inserrata* and cf. *Pseudictops tenuis*.

Characteristic fossils: *Asiostylops*, *Hsiuannania*, *Archaeolambda dayuensis*, *A. chijiangensis*, and *Ganolophus lanikenensis*.

The *Asiostylops* Interval Zone is best represented by the fauna from the Lannikeng Member of the Chijiang Formation, Chijiang Basin, Jiangxi Province. It is also represented by faunas from the Zhuguikeng Member, Nongshan Formation, Nanxiong Basin, Guangdong Province; the Lower Member of the Doumu Formation, Qianshan Basin, Anhui Province; and probably the Dazhang Formation, Tantou Basin, Henan Province.

Tong et al. (1979) subdivided the Chijiang Formation into two members, the lower, Lannikeng, and the upper, Wangwu (which is here assigned to the next zone). The taxa known from the Lannikeng Member (156.6 m thick) include *Asiostylops spanios*, *Hsiuannania minor*, cf. *Pseudictops tenuis*, Hyopsodontidae indet., *Pseudanisonchus antelios*, *Archaeolambda dayuensis*, *A. chijiangensis*, *Harpyodus decorus*, *Ganolophus lanikenensis*, *Archaeoryctes notialis*, and Insectivora indet. *Archaeolambda* is represented by advanced species.

Four taxa, *Hsiuannania tabiensis*, *Mimotona robusta*, *Allictops inserrata*, and *Obtususdon hanhuaensis*, from the Lower Member (about 1000 m thick) of the Doumu Formation, show that this fauna is typified by a prevalence of Asian endemic forms.

Tong et al. (1976) subdivided the Nongshan Formation into the lower, Zhuguikeng Member (about 159.5 m thick), and the upper, Datang Member (about 149.2 m; assigned here to the next zone). Faunas from the Zhuguikeng Member, containing ?*Pachyaena* sp., *Dilambda zhuguikengensis*, and Phenacolophidae n. gen. and sp., and the Dazhang Formation (Tong and Wang, 1979, 1980), containing *Pseudictops* indet. and Pastoralodontidae indet., are tentatively assigned to this zone.

Sinostylops *Interval Zone.*—This zone is defined to include faunas occurring during the time between the first appearance of *Sinostylops* and the first appearance of *Prodinoceras*. It is characterized as follows:

First appearance of: the arctostylopids *Sinostylops promissus*, *Bothriostylops notios*, *Bothriostylops* sp., and a new unnamed species of Arctosylopidae (Cifelli et al., 1989); *Heomys orientalis*, which is considered the most primitive species of Eurymylidae

(Li, 1977; Li and Ting, 1985); the tillodont *Interogale datangensis* (Ting and Zheng, 1989); and the edentate-like mammal *Ernanodon antelios* (Ding, 1987).

Characteristic fossils: *Heomys*, *Sinostylops promissus*, *Bothriostylops notios*, and *Archaeolambda tabiensis*.

The *Sinostylops* Interval Zone is best represented by the faunas from the Upper Member of the Doumu Formation, Qianshan Basin, Anhui Province; the Datang Member of the Nongshan Formation, Nanxiong Basin, Guangdong Province; and the Wangwu Member of the Chijiang Formation, Chijiang Basin, Jiangxi Province.

Taxa known from the Upper Member of the Doumu Formation include *Sinostylops promissus*, *Hyracolestes ermineus*, *Hsiuannania* sp., *Heomys orientalis*, *Mimotona wana*, and *Archaeolambda tabiensis*. *Heomys orientalis* shows derived features shared with rodents (Li and Ting, 1985).

Fossil mammals from the Datang Member include *Ernanodon antelios*, *Petrolemur brevirostre*, cf. *Huaiyangale leura*, *Haltictops mirabilis*, *H. meilingensis*, *Interogale datangensis*, Arctostylopidae n. gen. and sp., *Altilambda pactus*, *A. minor*, *Minchenella grandis*, *Radinskya yupingae*, and *Yuelophus validus*. This fauna is characterized by a diverse group of pastoralodontid pantodonts and phenacolophids and by the appearance of an edentate-like animal, *Ernanodon antelios*, and the earliest well-documented perissodactyl-like animal, *Radinskya yupingae* (McKenna et al., 1989).

Three species of Arctostylopidae, *Allostylops periconotus*, *Bothriostylops notios*, and *Bothriostylops* sp., from the Wangwu Member show that Arctostylopidae were quite diverse during this zone.

The Taizicun Fauna.—Mammalian species known from the Taizicun Formation include Multituberculata indet., ?Eurymylidae indet., *Pseudictops chaii*, Mesonychidae indet., *Archaeolambda* cf. *planicanina*, *Dilambda speciosa*, *Tienshanilophus subashiensis*, *T. lianmuqinensis*, *T. shengjinkouensis*, *Prodinoceras diconicus*, *P. turfanense*, *P. primigenum*, and *P. simplum* (Tong, 1978). This fauna is characterized by:

First appearance of: Dinocerata, represented by *Prodinoceras diconicus*, *P. turfanense*, *P. primigenum, and P. simplum*; the pseudictopid *Pseudictops chaii*; the archaeolambdid *Archaeolambda* cf. *planicanina*; and the first Cenozoic record of Multituberculata in Asia, represented by an indeterminate genus and species.

Tong (1978:98) considered this fauna to be "ba-

sically comparable to those from Gashato Formation and Naran Bulak layer," and that "the age of Taizicun fauna should be equivalent to Gashato and Naran Bulak faunas, or might be slightly older than them, because some species in the Taizicun fauna are more primitive than those in the Gashato and Naran Bulak." The Taizicun fauna probably represents the youngest fauna assigned here to the Nongshanian Land Mammal Age. Biostratigraphic relationships among the Taizicun fauna and those assigned below to the Gashatan Land Mammal Age require further investigation.

GASHATAN LAND MAMMAL AGE

The term "Gashato" was first used by Matthew and Granger (1925:1) for beds found to be "resting unconformably upon these Cretaceous beds," and which "yielded the interesting primitive mammalian fauna" found in southern Mongolia. Matthew et al. (1929) suggested that the Gashato fauna is late Paleocene in age. Romer (1966:335) proposed the term "Gashatan" for the Asian late Paleocene mammal age, and correlated the "Gashatan" with the North American Tiffanian and the European Thanetian. The Gashatan was defined by Szalay and McKenna (1971:313) as "the joint overlapping time ranges of *Palaeostylops*, *Pseudictops*, *Prionessus*, and *Eurymylus*," an interval considered by these workers to be "latest Paleocene in age" (Szalay and McKenna, 1971:281). Li and Ting (1983) suggested the term "Bayanulanian" as a tentative "Chinese Provincial Age" in their correlation table, in which "Bayanulanian" straddled a line between the late Paleocene "Nongshanian" and the early Eocene "Lingchan." Here, I advocate continued use of the name Gashatan for the latest Paleocene land mammal age because of its priority.

In recent years, paleontological expeditions by the American Museum of Natural History and the Mongolian Academy of Science have greatly improved collections of Gashatan mammals, both in quantity and quality. The Bayan Ulan fauna is currently under study (Zhai and Meng, 1995; Meng et al., 1998). This work will certainly clarify our understanding of the Gashatan Land Mammal Age.

Definition and Characterization

The Gashatan Land Mammal Age is defined here to include the time between the first appearance of the order Rodentia, represented by *Tribosphenomys*, and the first appearance of the order Perissodactyla, represented by *Orientolophus*. Although the earliest appearance of Rodentia is chosen here to define the

onset of the Gashatan, rodents have not been discovered in either the Gashato or the Naran faunas to date. As such, revision of the definition of the Gashatan may eventually become necessary. Subdivision of the Gasahatan is premature at this time. The Gasahatan Land Mammal Age is characterized as follows:

First appearance of: order Rodentia, represented by *Tribosphenomys minutus* (Meng et al., 1994); the pantodont family Coryphodontidae, represented by *Coryphodon tsaganensis*; the arctostylopids *Palaeostylops iturus* and *Gashatostylops macrodon*.

Last occurrence of Pseudictopidae and Pastoralodontidae.

Characteristic fossils: *Prionessus lucifer*, *Pseudictops lophiodon*, *Eurymylus laticeps*, *Palaeostylops iturus*, *Gashatostylops macrodon*, *Archaeolambda planicanina*, *Coryphodon tsaganensis*, *Prodinoceras*, and *Tribosphenomys minutus*.

The Gashatan Land Mammal Age is best represented by faunas from the Khashat (Gashato) Formation, Ulan Nur Basin, Mongolia; the Naran and Zhigden members of the Naran Bulak Formation, Nemegt Basin, Mongolia; the Naran Formation, Bugintsav Basin, Mongolia; and the Bayan Ulan and Nomogen formations of the Nomogen (Naomugen) area, Inner Mongolia (Nei Mongol Autonomous Region), China.

According to Dashzeveg (1982, 1988), late Paleocene and early Eocene strata in the Nemegt Basin comprise the Naran Bulak Formation. This unit is 80 m thick and can be subdivided into four members from bottom to top: the Zhigden (27 m) and the Naran (30 m), representing the late Paleocene; the Bumban (20 m), representing the early Eocene; and the Aguyt. In the Ulan Nur Basin, correlative strata comprise the Khashat (Gashato) Formation, which is subdivided into Member I (with Gashato fauna, 40 m thick) correlative with the Naran Member, Member II (11 m) correlative with the Bumban Member, and Member III (12 m) correlative with the Aguyt. In the Bugintsav Basin, fossils from the Bugin Member (20 m) of the Naran Bulak Formation indicate correlation with the Naran Member. Taxa known from the Naran Member and the Gashato fauna include *Prionessus lucifer*, *Dissacus indigenus*, *Eurymylus laticeps*, *Pseudictops lophiodon*, *Oxyaena* sp., "*Sinopa*" sp., *Gashatostylops macrodon*, *Palaeostylops iturus*, *Coryphodon tsaganensis*, *Pachyaena nemegetica*, *Archaeolambda planicanina*, and *Prodinoceras martyr*. Taxa known from the Zhigden Member include *Prodinoceras martyr*, *Archaeolambda planicanina*, *Gashatosty-*

lops macrodon, and *Ernanodon* sp. (Russell and Dashzeveg, 1985; Dashzeveg, 1988; Dashzeveg and Russell, 1988).

Qi (1979) listed the following species from the Bayan Ulan Formation: *Prionessus lucifer, Eomylus borealis, Pseudictops lophiodon, Pachyaena* sp., *Plagiocristodon serratus, Palaeostylops iturus, Gashatostylops macrodon, Pastoralodon lacustris, Prodinoceras efremovi, ?Lambdotherium* sp., and *?Heptodon* sp. Meng et al. (1994) recently published a new rodent species from this fauna, *Tribosphenomys minutus*. Two perissodactyl species, *?Lambdotherium* sp. and *?Heptodon* sp., were considered major evidence suggesting an early Eocene age for the formation (Qi, 1979; Li and Ting, 1983; Miao, 1988). *?Heptodon* sp. has been recently removed from the Bayan Ulan faunal list by Zhai and Meng (1995), because they consider it to have been reworked. *?Lambdotherium* sp. is based on very fragmentary material, thus its systematic position is questionable. The occurrences of the species *Prionessus lucifer, Pseudictops lophiodon, Gashatostylops macrodon*, and *Palaeostylops iturus* in the Bayan Ulan Formation indicate that the Bayan Ulan Formation is probably correlative with the Gashato Formation and the Naran Member of the Naran Bulak Formation.

Fossil mammals known from the Nomogen Formation are: *Prionessus lucifer, Sphenopsalis nobilis, Lambdopsalis bulla, Sarcodon pygmaeus, Eomylus borealis, Pseudictops lophiodon, ?Dissacus* sp., *Plagiocristodon serratus, Palaeostylops iturus, Gashatostylops macrodon, Pastoralodon lacustris, Convallisodon convexus, C. haliutensis*, and *?Rodentia* indet. (Chow and Qi, 1978). Seven of the 14 taxa (50%) from the nearby Bayan Ulan Formation are also known from the Nomogen Formation. This suggests that the Nomogen Formation is probably correlative with or slightly older than the Bayan Ulan Formation, depending on whether *?Lambdotherium* sp. from the Bayan Ulan Formation (Qi, 1979) is a true perissodactyl and on whether material supporting the appearance of the Rodentia in the Nomogen Formation is reliable.

In the Xuancheng Basin in Anhui Province, the Shuangtasi Formation unconformably overlies the Late Cretaceous Xuannan Formation (Qiu et al., 1977). Five taxa, *Hsiuannania maguensis, Dissacus magushanensis, Bothriostylops progressus, Archaeolambda yangtzeensis*, and *Wanotherium xuanchengensis*, have been reported from the Shuangtasi Formation to date (Tang and Yan, 1976; Xu, 1976a, 1976b; Yan and Tang, 1976; Huang, 1977, 1978; Zheng and Huang, 1986). *Hsiuannania maguensis* is among the most advanced Paleocene anagalids (Xu, 1976a). *Bothriostylops progressus* is a more advanced species than *B. notios* from the Wangwu Member of the Chijiang Formation (Tang and Yan, 1976; Zheng and Huang, 1986). Zheng and Huang (1986) suggested that the Shuangtasi Formation is early Eocene in age. Cifelli et al. (1989) considered it to be late Paleocene or early Eocene in age. *Wanotherium xuanchengensis* is a puzzling species from the Shuangtasi Formation; however, the material is too fragmentary for detailed identification. Two of the five genera from the Shuangtasi Formation are also found in the Naran Member of the Naran Bulak Formation, although no species is known to occur in both rock units. The Shuangtasi Formation is most likely correlative with the Naran Member, based on the occurrences of the advanced mesonychid *Dissacus maguensis* and the pantodont *Archaeolambda yangtzeensis*. This fauna is tentatively assigned to the Gashatan Land Mammal Age, but it is possibly somewhat younger.

In the Hengyang Basin in Hunan Province, two fossiliferous horizons are known from the Lingcha Formation. The upper of these has yielded a diverse fauna assigned to the Bumbanian Land Mammal Age, while the lower horizon has yielded *Archaeolambda* sp. A barren interval about 100 m thick separates these two fossiliferous layers (Li et al., 1979:73). In an initial report, Li et al. (1979) considered the *Archaeolambda*-bearing layer as either early Eocene or late Paleocene because *Archaeolambda* sp. is similar to *Archaeolambda planicanina*. Li and Ting (1983) called the *Archaeolambda*-bearing horizon ?Paleocene. In contrast, Zheng and Huang (1984) suggested that both the lower and upper fossiliferous horizons of the Lingcha Formation are early Eocene in age. Here, the lower part of the Lingcha Formation is tentatively assigned to the Gashatan.

ASIAN EARLY EOCENE LAND MAMMAL AGE

The history of the discovery of Asian early Eocene mammals can be traced back to the early 1960s, when new dinoceratan materials from the Xinyu Group, Yuanshui Basin, Jiangxi Province, were published (Chow, 1959; Chow and Tung, 1962), and the discovery of *Homogalax* from the Wutu Formation, Wutu Basin, Shangdong Province, was reported (Chow and Li, 1963). Important new discoveries from China have been added continuously ever since, including the mammals from the Niushan Formation, Niushan Basin, Shangdong Province (Chow and Li, 1965); Zhangshanji Formation, Laian Basin, Anhui Province (Zhai et al., 1976); Dabu and Shisanjianfang formations, Turfan Basin, Xinjiang Uygur Autonomous Region (Chow, 1960; Zhai, 1978a, 1978b); Lingcha Formation, Hengyang Basin, Hunan Province (Li, et al., 1979; Ding, 1995); and Yuhuangding Formation, Xichuan Basin, Henan Province (Xu et al., 1979). In Mongolia, important new finds from the Bumban Member of the Naran Bulak Formation in the Nemegt Basin, and Member II of the Khashat Formation in the Ulan Nur Basin have been published (Dashzeveg and McKenna, 1977; Dashzeveg, 1982, 1988, 1990a, 1990b). A small collection of fossil mammals from the Subathu Formation of India is considered early Eocene by Gingerich and Russell (1981) and Russell and Zhai (1987). This fauna includes marine mammals and proboscideans. Another fauna from the Kuldana Formation of Pakistan has been tentatively assigned to the early Eocene by Russell and Zhai (1987). The geographic distribution of early Eocene mammal localities of eastern Asia is shown in Figure 1.

BUMBANIAN LAND MAMMAL AGE

Romer (1966:335) proposed the name "Ulanbulakian" as the Asian early Eocene mammal age. He correlated the "Ulanbulakian" to the North American Wasatchian and the European Ypresian, Sparnacian, and Cuisian. Szalay and McKenna (1971: 281) referred Romer's "Ulanbulakian" to the "Gashatan." Li and Ting (1983) proposed the term "Lingchan" as a tentative early Eocene "Chinese Provincial Age." Russell and Zhai (1987:414) proposed the name "Bumbanian Mammal Age" for the Asian early Eocene, and the "Bumbanian" has since become widely accepted. I continue to use the term "Bumbanian" for the Asian early Eocene land mammal age.

Definition and Characterization

The Bumbanian Land Mammal Age is defined here to include the time between the first appearance of the order Perissodactyla, represented by the most primitive known tapiroid, *Orientolophus*, and the first appearance of rhinocerotoid perissodactyls, represented by *Hyrachyus*. The Bumbanian Land Mammal Age is characterized by the first appearance of the order Perissodactyla (*Orientolophus*, *Homogalax*), the rodent superfamily Ctenodactyloidea (*Cocomys*, *Bandaomys*), the rodent family Paramyidae (*Taishanomys*, *Acritoparamys*?), the family Hapalodectidae (*Hapalodectes*), and the primate *Altanius*. Coryphodontid pantodonts, rodents, and tapiroid perissodactyls are diverse and common during the Bumbanian Land Mammal Age. Arctostylopidae apparently became extinct during this interval.

Zonation

Three interval zones are recognized within the Bumbanian Land Mammal Age: the *Orientolophus* Interval Zone, the *Homogalax* Interval Zone, and the *Heptodon* Interval Zone (Fig. 2). Most mammalian faunas assigned to the Bumbanian Land Mammal Age occur in geographically isolated depositional basins, which has led to difficulty in determining the relative ages of strata and faunas. The zonation advocated here is based on genera of perissodactyls, because they appear to indicate distinctive evolutionary trends of early perissodactyls in Asia (Ting, 1993).

Orientolophus *Interval Zone.*—This zone is defined to include faunas occurring during the time between the first appearance of *Orientolophus* and the first appearance of *Homogalax*. It is characterized as follows:

First appearance of: the order Perissodactyla, represented by *Orientolophus hengdongensis* (Ting, 1993); the probable basal euprimate *Altanius orlovi* (Dashzeveg and McKenna, 1977; Gingerich et al., 1991); the rodent superfamily Ctenodactyloidea, represented by *Cocomys lingchaensis* (Dawson et al., 1984); and the family Hapalodectidae, represented by *Hapalodectes hetangensis* (Ting and Li, 1987).

Characteristic fossils: *Naranius*, *Cocomys*, *Tsagamys*, *Matutinia*, *Orientolophus*, *Hapalodectes*, and *Hyopsodus orientalis*.

The *Orientolophus* Interval Zone is best repre-

Age	Land Mammal Age	Asia	North America	Europe
M. Eocene				
Early Eocene	Bumbanian	—Hyrachyus modestus— Heptodon Interval Zone —Heptodon tienshanensis— Homogalax Interval Zone —Homogalax wutuensis— Orientolophus Interval Zone —Orientolophus hengdongensis—	Wasatchian: —Hyrachyus modestus— ?Lostcabinian Lysitean —Heptodon calciculus— Graybullian —Homogalax protapirinus— Sandcouleean	Cuisian ? Sparnacian
Paleocene — L.	Gashatan	Gashatan Faunas —Tribosphenomys minutus—	Clarkforkian: Cf3 —Hyracotherium sandrae— Cf2 —Phenacolemur praecox— —Esthonyx ancylion— Cf1 —Paramys atavus—	—Cymbalophus cuniculus—
	Nongshanian	? Taizicun Fauna —Prodinoceras diconicus— Sinostylops Interval Zone —Sinostylops promissus— Asiostylops Interval Zone —Asiostylops spanios—	Tiffanian	Thanetian
Paleocene — E.	Shanghuan	Archaeolambda Interval zone —Archaeolambda sp. n.— Bemalambda Interval Zone —Bemalambda nanhsiungensis—	Torrejonian	?Montian stage (or Danian substage)

Fig. 3.—Tentative intercontinental correlation of early Cenozoic Asian and North American land mammal ages with European stages.

sented by faunas from the Bumban Member of the Naran Bulak Formation, Nemegt Basin, Mongolia; and the upper part of the Lingcha Formation, Hengyang Basin, Hunan Province.

Dashzeveg (1982, 1988, 1990a, 1990b; Dashzeveg et. al., 1987) recently reported the following taxa from the Bumban Member of the Naran Bulak Formation: *Gomphos elkema*, *Archaeolambda* sp., *Arctostylops* sp., *Naranius infrequens*, *Bumbanius rarus*, *Oedolius perexiguus*, *Tsaganius ambiguus*, *Hyopsodus orientalis*, *Hapalodectes* sp., *Zagmys insolitus*, *Rhombomylus* sp., *Altanius orlovi*, *Alagomys inopinatus*, *Orogomys obscurus*, *Sharomys singularis*, *S. parvus*, *Kharomys mirandus*, *K. gracilis*, *Tsagamys subitus*, and *Ulanomys mirificus*. The perissodactyls *Hyracotherium gabuniai* and *Homogalax namadicus* from the Bumban Member have recently been referred to the genus *Orientolophus* by Ding (1995).

Fossil mammals known from the upper part of the Lingcha Formation (= the Hengdong fauna) include *Hsiangolestes youngi*, cf. *Naranius* n. sp., *Matutinia nitidulus*, *Hapalodectes hetangensis*, *Asiocoryphodon* sp., *Orientolophus hengdongensis*, "*Propachynolophus*" *hengyangensis*, *Cocomys lingchaensis*, cf. *Tsagamys* n. sp., and *Hunanictis inexpectatus* (Ting and Li, 1987; Ding, 1995). The occurrences of *Naranius*, *Tsagamys*, *Orientolophus*, and *Hapalodectes* in both the Bumban and Hengdong faunas suggest that they are probably equivalent in age.

Two taxa, *Coryphodon dabuensis* and *Prodinoceras xinjiangensis*, are reported from the Dabu Formation (22 m in thickness), Turfan Basin, Xinjiang Uygur Autonomous Region. According to Zhai (1978a), *C. dabuensis* is close to the European *C. eocaenus* and North American *C. proterus* in terms of its dentition. Zhai (1978a:105) suggested

Table 1.—*Fossil mammals known from faunas assigned to the Shanghuan Land Mammal Age (abbreviations are: SH, Shanghu Formation; WH, Wanghudun Formation; SZ, Shizikou Formation; ZS, Zaoshi Formation; FG, Fangou Formation; GY, Gaoyugou Formation).*

Anagalida
  Anagalidae
    Linnania lofoensis SH
    Linnania qinglingensis FG
    Huaiyangale chianshanensis WH
    Huaiyangale sp. WH
    Diacronus wanghuensis WH
    Eosigale gujingensis WH
    Qipania yui WH
    Wanogale hodungensis WH
    Anaptogale wanghoensis WH
    Chianshania gianghuaiensis WH
    Stenanagale xiangensis ZS

  Astigalidae
    Astigale nanxiongensis SH
    Astigale wanensis WH
    Zhujegale lirenensis SH
    Zhujegale jintangensis SH

  Pseudictopidae
    Anictops tabiepedis WH
    Anictops aff. *tabiepedis* WH
    Paranictops majuscula WH
    Paranictops sp. WH
    ?*Paranictops* sp. WH
    Cartictops caninia WH

?Simplicidentata
  Eurymylidae
    Heomys sp. WH

?Duplicidentata
  Mimotonidae
    Mimotona wana WH
    Mimotona sp. WH

Carnivora
  Miacidae
    Pappictidops acies SH
    Pappictidops obtusus SH
    Pappictidops orientalis WH

Condylarthra
  Hyopsodontidae
    Yuodon protoselenoides SH
    Palasiodon siurenensis SH

  Periptychidae
    ?*Ectoconus* sp. SH

Acreodi
  Mesonychidae
    Yantanglestes feiganensis SH
    Yantanglestes conexus WH
    Dissacusium shanghoensis SH
    Hukoutherium ambigum SH
    Hukoutherium shimnenensis FG

Table 1.—*Continued.*

    Dissacus rotundus ZS
    Mesonychidae indct. GY
Tillodontia
  Esthonychidae
    Lofochaius brachyodus SH
    Anchilestes impolitus WH
    Meiostylodon zaoshiensis ZS
?Tillodontia
    Dysnoetodon minuta SH
Insectivora
  Micropternodontidae
    Prosarcodon lonanensis FG
Primates
  ?Omomyidae
    Decoredon anhuiensis WH
Pantodonta
  Bemalambdidae
    Bemalambda nanhsiungensis SH, ZS
    Bemalambda pachyoesteus SH
    Bemalambda crassa SH
    Bemalambda shizikouensis SH
    Bemalambda sp. SH, WH
    Bemalambda indet. WH, ZS, GY, FG
    Hypsilolambda chalingensis ZS
    Hypsilolambda impensa ZS
    Hypsilolambda spp. ZS

  Archaeolambdidae
    Archaeolambdidae indet. ZS

  Pastoralodontidae
    Altilambda pactus WH
    Altilambda tenuis WH
    Altilambda yujingensis WH

  Harpyodidae
    Harpyodus euros WH

  Plethorodontidae
    Plethorodon chienshanensis WH

Order Uncertain
    Obtususdon hanhuaensis WH

  Didymoconidae
    Zeuctherium niteles WH

"*Pyrodon* from the Dabu Formation is more advanced than *Prodinoceras* from Taizicun and Gashato formations." The age of the Dabu Formation requires further study.

Two species, *Phenaceras lacustris* and *Ganatherium australis* (Tong, 1979*b*), were reported from the Pinghu Formation (200–300 m in thickness). Both of these species were referred to *Prodinoceras* by Schoch and Lucas (1985), who also considered *G. australis* a junior subjective synonym of *Phen-*
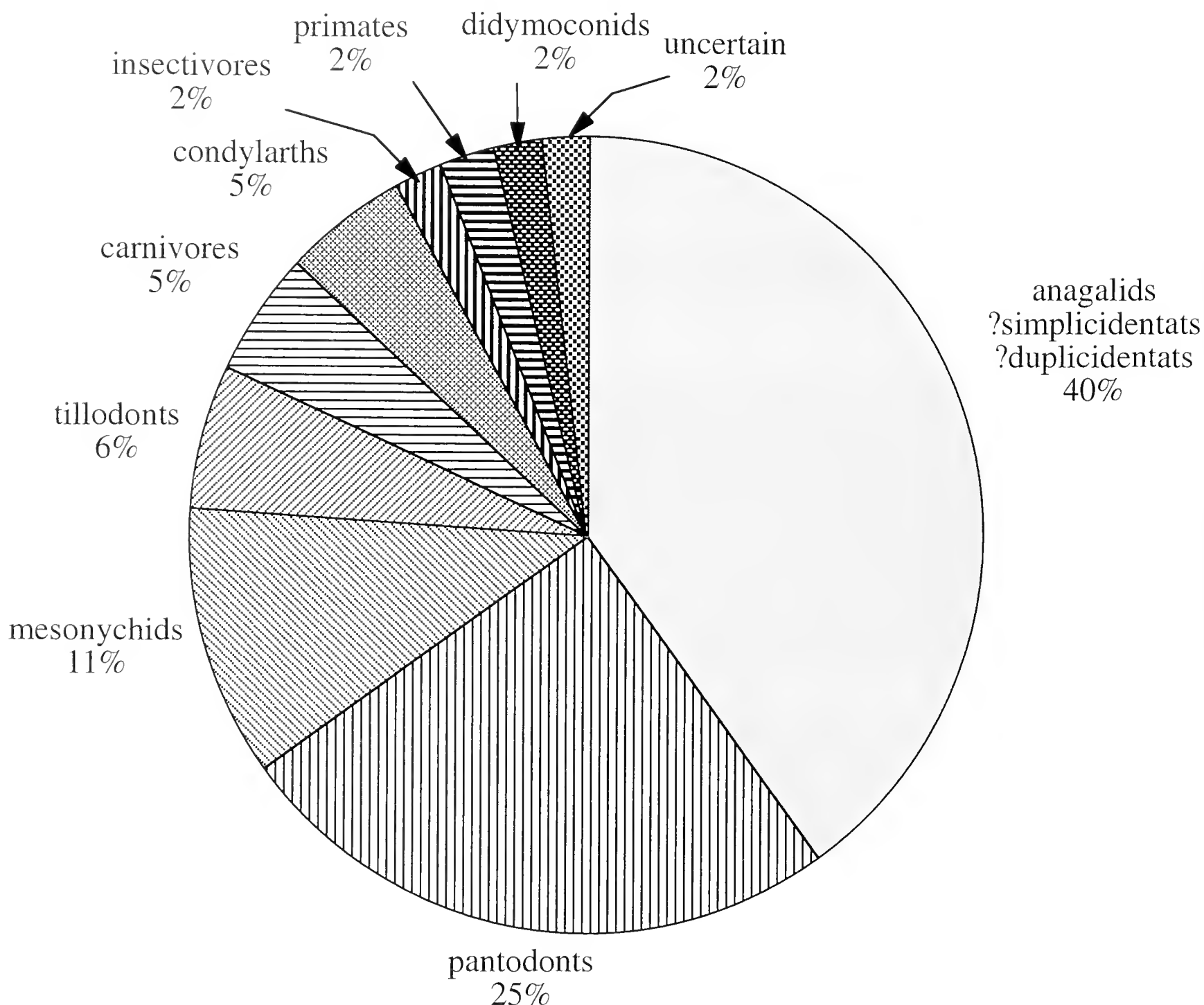
Fig. 4.—Species-level diversity of mammalian higher taxa in the Shanghuan Land Mammal Age.

aceras lacustris. The Pinghu fauna is tentatively assigned to the *Orientolophus* Interval Zone.

Homogalax *Interval Zone.*—This zone is defined to include faunas occurring during the time between the first appearance of *Homogalax* and the first appearance of *Heptodon*. The zone is currently represented only by the fauna from the Wutu Formation, Wutu Basin, Shandong Province. This diverse mammalian fauna is still being collected and described by Y. S. Tong, J. W. Wang, and their colleagues (Tong and Wang, 1993, 1994; Beard and Wang, 1995; Tong and Dawson, 1995). Here, the Wutu fauna is considered to be slightly younger than the Hengdong and Bumban faunas, mainly on the basis of the occurrence of a more advanced perissodactyl species, *Homogalax wutuensis*, in the

Wutu fauna. The *Homogalax* Interval Zone is characterized as follows:

First appearance of: the perissodactyl family Isectolophidae, represented by *Homogalax wutuensis* (Chow and Li, 1963); the rodent family Paramyidae, represented by *Taishanomys changlensis* and *Acritoparamys? wutui* (Tong and Dawson, 1995).

Last Asian occurrence of Multituberculata, represented by *Mesodmops dawsonae* (Tong and Wang, 1994).

Characteristic fossils: *Mesodmops dawsonae, Changelestes dissetiformis, Chronolestes simul, Carpocristes oriens, Bandaomys zhonghuaensis, Taishanomys changlensis, Acritoparamys? wutui, Homogalax wutuensis.*

Heptodon *Interval Zone.*—This zone is defined

Table 2.—*Fossil mammals known from faunas assigned to the Nongshanian Land Mammal Age (abbreviations are: NS, Nongshan Formation; CJ, Chijiang Formation; DM, Doumu Formation; DZ, Dazhang Formation;, TZ, Taizicun Formation).*

Table 2.—*Continued.*

Multituberculata
  Multituberculata indet. TZ

?Edentata
  Ernanodontidae
    Ernanodon antelios NS

Insectivora
  Family indet.
    Hyracolestes ermineus DM
    Insectivora indet. CJ

?Primates
  Adapidae
    Petrolemur brevirostre NS

Anagalida
  Anagalidae
    Hsiuannania tabiensis DM
    Hsiuannania minor CJ
    Hsiuannania sp. DM
    cf. *Huaiyangale leura* NS

  Pseudictopidae
    Hartictops mirabilis NS
    Hartictops meilingensis NS
    Allictops inserrata DM
    Pseudictops chaii TZ
    cf. *Pseudictops tenuis* CJ
    Pseudictopidae indet. DZ

?Simplicidentata
  Eurymylidae
    Heomys orientalis DM
    Eomylus borealis DM
    Eurymyloidea indet. DZ
    ?Eurymylidae indet. TZ

?Duplicidentata
  Mimotonidae
    Mimotona wana DM
    Mimotona robusta DM

Tillodonta
  Esthonychidae
    Interogale datangensis NS

Acreodi
  Mesonychidae
    Yantanglestes datangensis NS
    Jiangxia chaotoensis CJ
    ?*Dissacus* sp. CJ
    ?*Pachyaena* sp. NS
    Mesonychidae indet. TZ

Condylarthra
  Hyopsodontidae
    Hyopsodontidae indet. CJ

Periptychidae
  Pseudanisonchus antelios CJ

Arctostylopida
  Arctostylopidae
    Asiostylops spanios CJ
    Allostylops periconotus CJ
    Bothriostylops notios CJ
    Bothriostylops sp. CJ
    Sinostylops promissus DM
    Arctostylopidae n. gen. and sp. NS

Pantodonta
  Archaeolambdidae
    Archaeolambda dayuensis CJ
    Archaeolambda tabiensis DM
    Archaeolambda sp., cf. *A. planicanina* CJ, TZ
    Archaeolambda sp. CJ
    Nanlingilambda chijiangensis CJ
    Nanlingilambda sp. NS

  Pastoralodontidae
    Altilambda pactus NS
    Altilambda minor NS
    Altilambda sp. NS
    Pastoralodontidae indet. DZ

  Harpyodidae
    Harpyodus decorus CJ

  Pantolambdodontidae
    Dilambda speciosa TZ
    Dilambda zhuguikengensis NS

  Phenacolophidae
    Minchenella grandis NS
    Yueloplus validus NS
    Ganoloplus lanikenensis CJ
    Tienshaniloplus subashiensis TZ
    Tienshaniloplus lianmuqinensis TZ
    Tienshaniloplus shengjinkouensis TS
    Phenacolophidae n gen. and sp. NS

  ?Phenacolophidae
    Radinskya yupingae NS

Dinocerata
  Prodinoceratidae
    Prodinoceras diconicus TZ
    Prodinoceras turfanense TZ
    Prodinoceras primigenum TZ
    Prodinoceras simplum TZ

Order Uncertain
    Obtususdon hanhuaensis DM

  Didymoconidae
    Archaeoryctes notialis CJ

condylarths uncertain
3%   2%

insectivores
3%

dinoceratans
6%

mesonychids
8%

arctostylopids
9%

edentates
2%
?primates
2%

anagalids
?simplicidentats
?duplicidentats
didymoconids
27%

tillodonts
2%
multituberculates
2%

pantodonts
34%
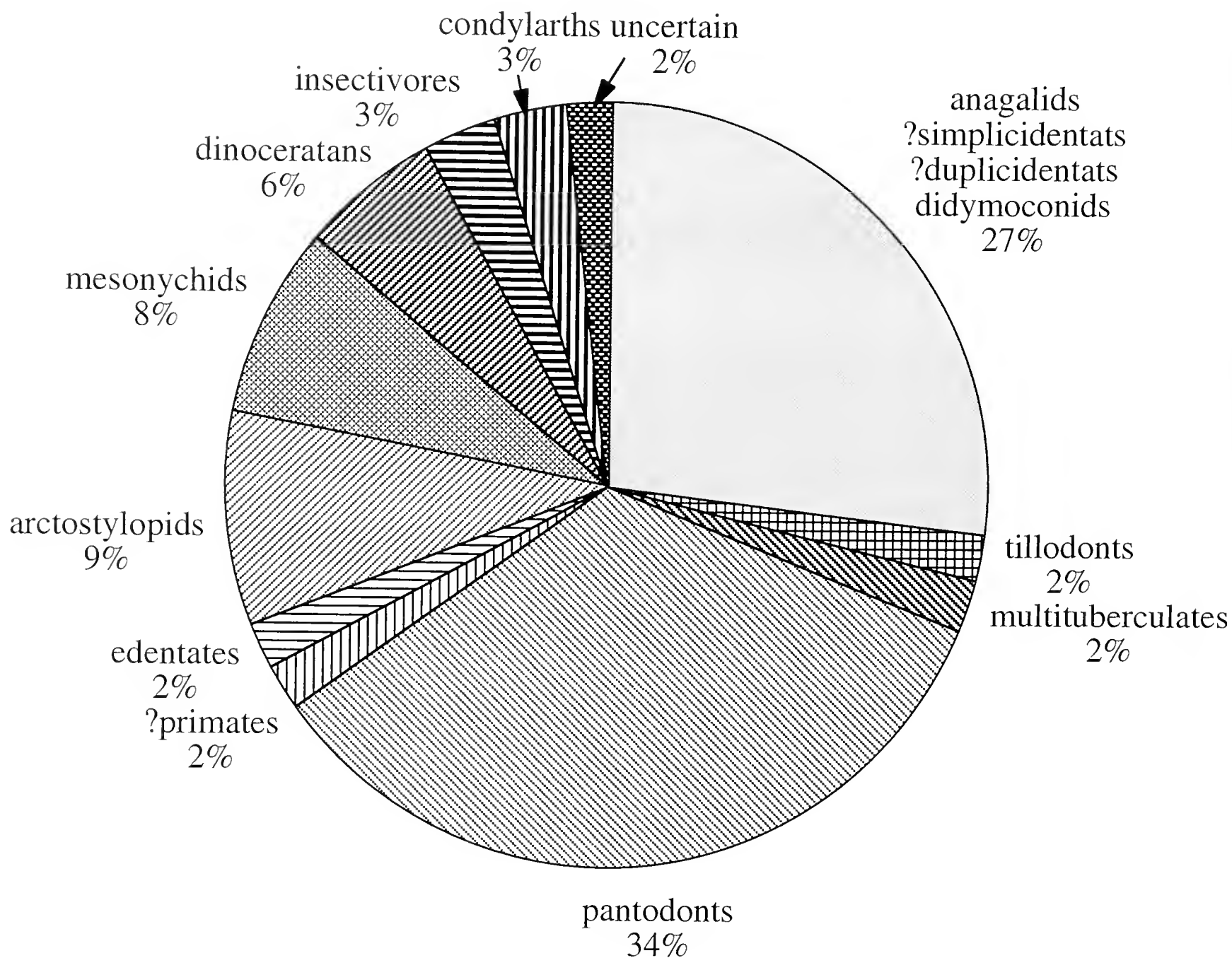
Fig. 5.—Species-level diversity of mammalian higher taxa in the Nongshanian Land Mammal Age.

to include faunas occurring during the time between the first appearance of *Heptodon* and the first appearance of *Hyrachyus* (Qi, 1987). The zone is characterized as follows:

First appearance of: the perissodactyl family Helaletidae, represented by *Heptodon* (Chow and Li, 1965; Zhai, 1978*b*); and the advanced rodent *Advenimus* (Dawson et al., 1984).

Last occurrence of Arctostylopida.

Characteristic fossils: *Heptodon, Rhombomylus, Coryphodon flerowi, C. ninchiashanensis, Asiocoryphodon, Miacis tenuis,* and *Advenimus.*

The *Heptodon* Interval Zone is carpresented by faunas from the Shisanjianfang Formation, Turfan Basin, Xinjiang Uygur Autonomous Region; the Niushan Formation, Niushan Basin, Shandong Province; the Yuhuangding Formation, Xichuan Basin, Henan Province; the Zhangshanji Formation, Laian Basin, Anhui Province; and probably the Nin-

gjiashan Member of the Xinyu Group, Yuanshui Basin, Jiangxi Province.

The Shisanjianfang Formation is about 272 m thick. Fossils occur between 18 and 30 m from the top. Five taxa have been reported to date, including: *Coryphodon* sp., *Rhombomylus turpanensis, Hyopsodus* sp., *Heptodon tienshanensis,* and *Anatolostylops dubius* (Zhai, 1978*b*).

Only one species, *Heptodon niushanensis,* has been recovered from the Niushan Formation (Chow and Li, 1965). *Heptodon niushanensis* is slightly larger than *H. turpanensis* from the Shisanjianfang Formation. However, this size difference may not reflect a significant stratigraphic difference.

Fossil mammals known from the Yuhuangding Formation (400–900 m thick) include *Asiocoryphodon conicus, A. lophodontus,* Dinocerata indet., *Advenimus hupeiensis, Rhombomylus* sp., and cf. *Heptodon* sp. (Chow et al., 1973*a*; Gao, 1976; Xu,

Table 3.—*Fossil mammals known from faunas assigned to the Gashatan Land Mammal Age (abbreviations are: BU, Bayan Ulan Formation; NM, Nomogen Formation; ST, Shuangtasi Formation; ZG, Zhigden Member; NR, Naran Member; GS, Gashato; BT, Bugin Member).*

Multituberculata
  Taeniolabididae
    Prionessus lucifer BU, NR, GS, NM
    Lambdopsalis bulla BU
    Sphenopsalis nobilis NM
?Edentata
  Ernanodontidae
    Ernanodon sp. ZG
Anagalida
  Zalambdalestidae
    Praolestes nanus GS
  Anagalidae
    Hsiuannania maguensis ST
    Khashanagale zofiae GS
    ?Khashanagale sp. GS
  Pseudictopidae
    Pseudictops lophiodon BU, NR, GS
?Simplicidentata
  Eurymylidae
    Eurymylus laticeps NR, GS
    Khaychina elongata BT
    Eomylus borealis BU
    Eomylus zhigdenensis ZG, NR
    Amar aleator ZG
    Zagmys insolitus BG
Acreodi
  Mesonychidae
    Dissacus magushanensis ST
    Dissacus indigenus NR
    Dissacus sp. GS, NM
    Plagiocristodon serratus BU, NM
    Pachyaena nemegetica NR
    Pachyaena sp. BU
Creodonta
  Oxyaenidae
    Oxyaena sp. NR
Insectivora
  Micropternodontidae
    Sarcodon pygmaeus GS, NM
    Hyracolestes ermineus GS
    "*Sinopa*" sp. NR
Arctostylopida
  Arctostylopidae
    Bothriostylops progressus ST
    Palaeostylops iturus BU, NM, GS
    Gashatostylops macrodon BU, ZG, NR, GS, NM
Pantodonta
  Archaeolambdidae
    Archaeolambda yangtzeensis ST

Table 3.—*Continued.*

    Archaeolambda planicanina ZG, NR
    Archaeolambda trofimovi BT
  Pastoralodontidae
    Pastoralodon lacustris BU
    Convallisodon convexus NM
    Convallisodon haliutensis NM
  Pantolambdodontidae
    Pantolambdodon lophiodon NM
  Coryphodontidae
    Coryphodon tsaganensis NR
Dinocerata
  Prodinoceratidae
    Prodinoceras efremovi BU
    Prodinoceras martyr NR, GS, ZG
    Prodinoceras sp. BU, BT
?Perissodactyla
  Brontotheriidae
    ?Lambdotherium sp. BU
  Helaletidae
    ?Heptodon sp. BU
Rodentia
  ?Alagomyidae
    Tribosphenomys minutus BU
    Rodentia indet. NM
Order Uncertain
    Wanotherium xuanchengensis ST

1976; Xu et al., 1979). Xu et al. (1979) proposed that the Yuhuangding Formation is late early Eocene and about equivalent to the Shisanjianfang Formation and Ningjiashan Member of the Xinyu Formation, and younger than the Lingcha Formation. Li and Ting (1983) suggested that the Yuhuangding Formation is late early Eocene or early middle Eocene. The records of *Heptodon* and *Rhombomylus* from the Yuhuangding Formation are similar to those known from the Shisanjianfang and Niushan formations, suggesting that the Yuhuangding Formation correlates with the Shisanjianfang and Niushan formations.

Only one species, *Rhombomylus laianensis*, has been reported from the Zhangshanji Formation (108.6 m thick) (Zhai et al., 1976). Zhai et al. (1976) suggested an earlier Eocene age for the Zhangshanji Formation. Li and Ting (1983) and later Russell and Zhai (1987) suggested that this formation is early Eocene. *Rhombomylus laianensis* is basically comparable to *R. turpanensis* from the Shisanjianfang Formation. The Zhangshanji For-

Table 4.—*Fossil mammals known from faunas assigned to the Bumbanian Land Mammal Age (abbreviations are: LC, Lingcha Formation; DB, Dabu Formation; PH, Pinghu Formation; WT, Wutu Formation; YH, Yuhuangding Formation; ZS, Zhangshanji Formation; NS, Niushan Formation; NJ, Ningjiashan Member; SS, Shisanjianfang Formation; BB, Bumban Member; UN, Members II and III; AT, Aguyt Member).*

Insectivora
  Nyctitheriidae
    Bumbanius rarus BB
    Oedolius perexiguus BB
    Nyctitheriidae indet. BB
    Lipotyphla indet. BB
  Palaeoryctidae
    Naranius infrequens BB
    cf. *Naranius* sp. LC
    Tsaganius ambiguus BB
  Pantolestidae
    Pantolestidae indet. BB
  Micropternodontidae
    Hsiangolestes youngi LC
    cf. *Hyracolestes* sp. BB
  Changlelestidae
    Changlelestes dissetiformis WT
  Insectivora n. gen. and sp. LC
?Simplicidentata
  Eurymylidae
    Zagmys insolitus BB
    Gomphos elkema BB, UN, AT
    Matutinia nitidulus LC
    Rhombomylus laianensis ZS
    Rhombomylus turpanensis SS
    Rhombomylus sp., cf. *R. turpanensis* YH
    Rhombomylus sp. BB
Acreodi
  Hapalodectidae
    Hapalodectes hetangensis LC
    Hapalodectes sp. BB
Condylarthra
  Hyopsodontidae
    Hyopsodus orientalis BB
    Hyopsodus sp. WT, SS
Arctostylopida
  Arctostylopidae
    Anatolostylops dubius SS
    Arctostylops sp. BB
Pantodonta
  Archaeolambdidae
    Archaeolambda sp. BB, LC
  Coryphodontidae
    Coryphodon dabuensis DB
    Coryphodon flerowi YH
    Coryphodon ninchiashanensis NJ
    Coryphodon sp. SS, NJ

Table 4.—*Continued.*

    Asiocoryphodon conicus YH
    Asiocoryphodon lophodontus YH
    Asiocoryphodon sp. LC
    Heterocoryphodon sp. WT
    Manteodon sp., cf. *M. youngi* YH
Dinocerata
  Prodinoceratidae
    Prodinoceras lacustris PH
    Prodinoceras australis PH
    Prodinoceras sinyuensis NJ
    Prodinoceras xinjiangensis DB
    ?*Gobiatherium* sp. YH
Carnivora
  Miacidae
    Miacis tenuis NJ
Perissodactyla
  ?Isectolophidae
    Orientolophus hengdongensis LC
    ?*Orientolophus namadicus* BB
    ?*Orientolophus gabuniai* BB
    Homogalax wutuensis WT
  Helaletidae
    Heptodon niushanensis NS
    Heptodon tianshanensis SS
    cf. *Heptodon* sp. YH
    ?*Heptodon* sp. NJ
  Family uncertain
    Propachynolophus hengyangensis LC
Rodentia
  Alagomyidae
    Alagomys inopinatus BB
    Alagomys oriensis WT
  ?Yuomyidae
    Bandaomys zhonghuaensis WT
  Paramyidae
    Taishanomys changlensis WT
    Acritoparamys? *wutui* WT
  Cocomyidae
    Cocomys lingchaensis LC
    Sharomys singularis BB
    Sharomys parvus BB
    Kharomys mirandus BB
    Kharomys gracilis BB
    Tsaganys subitus BB
    cf. *Tsaganys* n. sp. LC
    Ulanomys mirificus BB
    Advenimus hupeiensis YH
  Orogomyidae
    Orogomys obscurus BB
Primates
  Omomyidae
    Altanius orlovi BB

Table 4.—*Continued.*

Carpolestidae
    Chronolestes simul WT
    Carpocristes oriens WT
Order Uncertain
  Didymoconidae
    Hunanictis inexpectatus LC
Multituberculata
  Neoplagiaucidae
    Mesodmops dawsonae WT

mation is most likely correlative to the Shisanjian-fang Formation.

The fauna from the Ningjiashan Member of the Xinyu Group contains "*Coryphodon*" *ninchiashanensis*, *Coryphodon* sp., *Prodinoceras sinyuensis*, *Miacis tenuis*, and ?*Heptodon* sp. The Ningjiashan Member was considered early Eocene by Chow and Tung (1962, 1965), Chang and Tung (1963), Li and Ting (1983), and Russell and Zhai (1987). Zheng et al. (1975) suggested that the Ningjiashan Member is very early Eocene. The materials representing ?*Heptodon* sp. and *Prodinoceras sinyuensis* are poorly preserved. *Miacis tenuis* (Zheng et al., 1975) is similar to *M. winkleri* from the Willwood Formation of North America according to Gingerich (1983). The occurrences of *M. tenuis* and "*C.*" *ninchiashansis* may indicate that the Ningjiashan Member is older than the Yuhuangding Formation. However, ?*Heptodon* sp., an advanced perissodactyl, is similar to that in the Yuhuangding Formation. Correlation of the Ningjiashan Member remains uncertain.

CORRELATION WITH NORTH AMERICAN AND EUROPEAN LAND MAMMAL AGES

The North American Paleocene land mammal ages are the Puercan, Torrejonian, Tiffanian, and Clarkforkian (Archibald et al., 1987) (Fig. 3). In Asia the Shanghuan, currently the earliest Cenozoic land mammal age, is best represented by the Shanghu and Wanghudun faunas. Zhou et al. (1977:9) proposed that "the upper limit of the Shanghu fauna is probably not beyond the Torrejonian" and "the lower three layers are probably close to the Dragonian." According to Archibald et al. (1987), the "Dragonian" is now included as the first interval zone of the Torrejonian Land Mammal Age. Zhexi Luo (personal communication, 1995) suggests that the base of the Shanghu Formation is possibly correlative with the Puercan, based on his current study of a condylarth from the Shanghu Formation. Zhao et al. (1991) reported the first paleomagnetic results from the Nanxiong Basin, in which the Cretaceous–Tertiary boundary was interpolated to lie "20 m above the base of Shanghu Formation" (p. 14). These workers also mentioned that "the lower part of the Shanghu Formation seems to be very close to the beginning of Paleocene" (p. 14). Qiu et al. (1977) suggested that the Wanghudun Formation is middle Paleocene; however, its Lower Member might be early Paleocene. The compositions of both Shanghu and Wanghudun faunas are very different from those of the Puercan: no genera or even families are comparable. Correlation of North American Puercan faunas with the Asian sequence of land mammal ages recognized here remains an open question. The composition of the Shanghu and Wanghudun faunas also differs from that of North American Torrejonian faunas. The similar occurrences of *Dissacus* and primitive pantodonts in both the Shanghuan and the Torrejonian indicate that the Shanghuan is probably partly or wholly correlative with the Torrejonian.

The faunal composition of the Nongshanian differs from that of the Tiffanian. The first occurrence of the orders Arctostylopida and Dinocerata in both the Nongshanian and the Tiffanian may indicate that the Nongshanian correlates with the Tiffanian.

The Gashatan is correlated with the Clarkforkian, mainly on the basis of the first occurrence of the order Rodentia and the pantodont family Coryphodontidae in both the Gashatan and the Clarkforkian.

The Wasatchian Land Mammal Age is the first Eocene land mammal age in North America. The traditional subdivision of the Wasatchian into three subages—the Graybullian, the Lysitean, and the Lostcabinian—has been considerably revised in the last decade (Rose, 1981; Stucky, 1984; West et al., 1987; Gingerich, 1989). West et al. (1987) considered that the early Wasatchian includes the Sandcouleean (the earliest Wasatchian) and Graybullian, and is characterized by "multituberculates, *Homogalax, Phenacodus, Coryphodon, Hyracotherium, Hyopsodus, Haplomylus, Ectocion, Pelycodus*, and *Diacodexis*" (West et al., 1987:86). According to
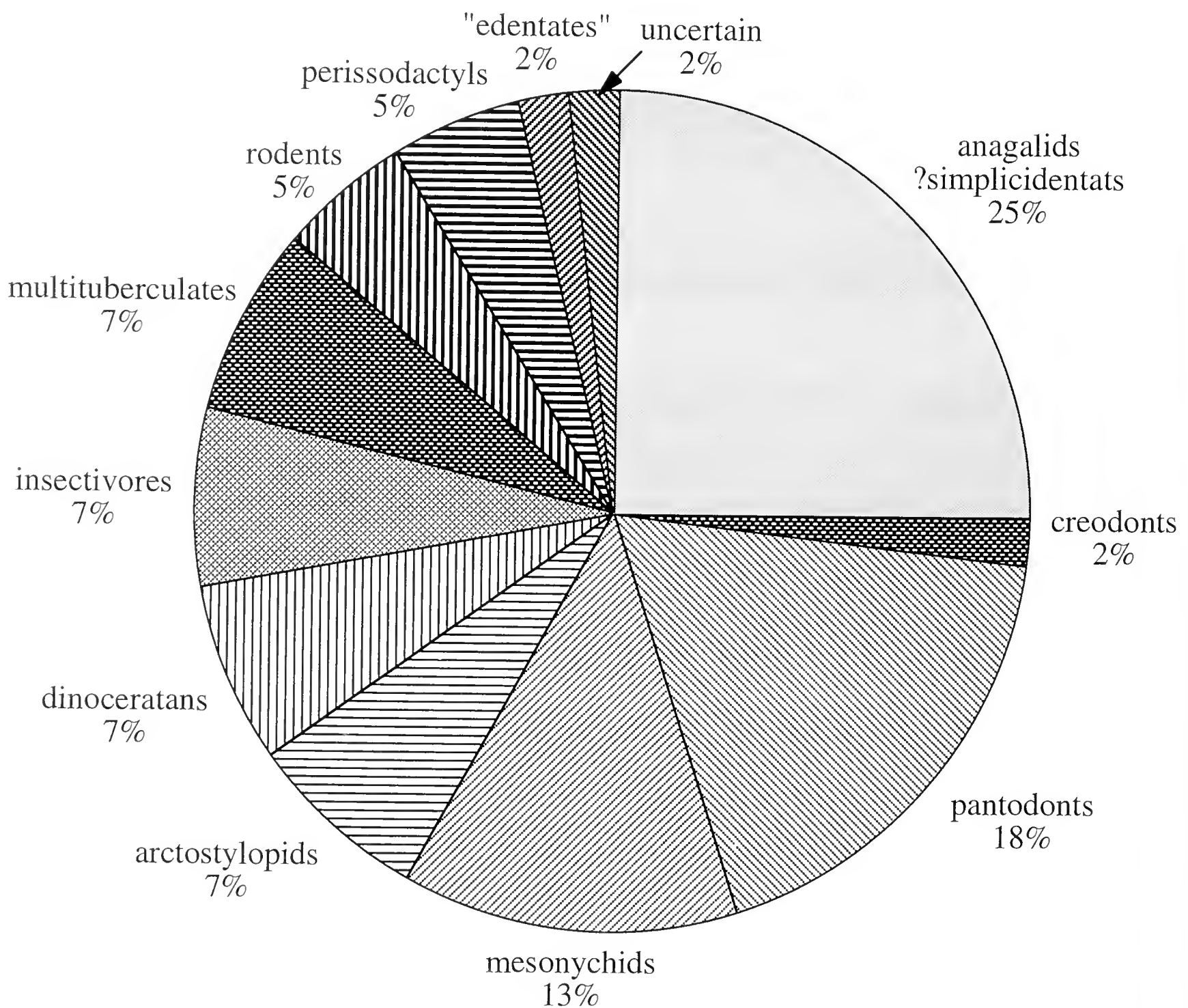
Fig. 6.—Species-level diversity of mammalian higher taxa in the Gashatan Land Mammal Age.

Gingerich (1991:206), the early Wasatchian is composed only of the Sandcouleean, defined by the first appearance of *Hyracotherium sandrae*; the middle Wasatchian is represented by the Graybullian (first appearance of *Homogalax protapirinus*); the late Wasatchian is represented by the Lysitean (first appearance of *Heptodon calciculus*) and the Lostcabinian (first appearance of *Lambdotherium primaevum*).

Dashzeveg (1982, 1988) proposed that in central Asia, the Paleocene–Eocene boundary is beneath the Bumban Member of the Naran Bulak Formation, which "displays almost synchronous entry of condylarths (*Hyopsodus*), primates (*Altanius*), and perissodactyls (*Hyracotherium* and *Homogalax*)" as in the Graybullian fauna. He further indicated that the "Gray Bull and Bumban faunas appear to be practically contemporaneous and are correlated with the Sparnacian fauna of West European Meudon" (Dashzeveg, 1988:473).

Three successive interval zones are recognized within the Bumbanian Land Mammal Age here. The *Orientolophus* Interval Zone is considered to be correlative with the Sandcouleean, because *Orientolophus hengdongensis* and *Hapalodectes hetangensis* are more primitive, respectively, than *Cardiolophus radinskyi* and *H. leptognathus* from the Graybullian. The *Homogalax* Interval Zone is correlated with the Graybullian subage of the Wasatchian, mainly because *H. wutuensis* is comparable to *H. protapirinus* from the Graybullian. The *Heptodon* Interval Zone is correlated with the Lysitean and Lostcabinean, based on the shared occurrence of *Heptodon*.
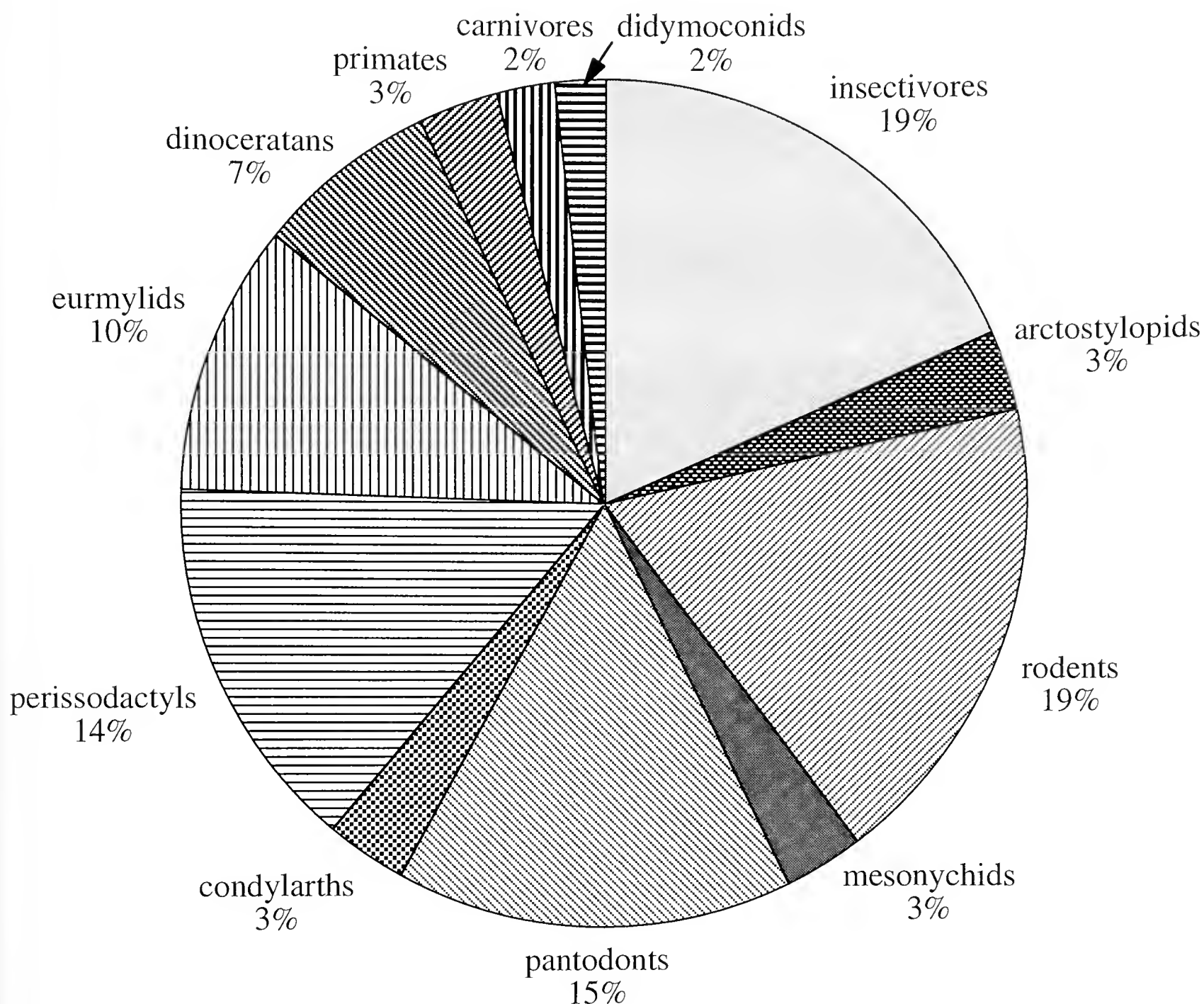
Fig. 7.—Species-level diversity of mammalian higher taxa in the Bumbanian Land Mammal Age.

POSSIBLE EARLY MIGRATION BETWEEN ASIA AND OTHER CONTINENTS

Shanghuan faunas (Table 1) are characterized by the prevalence of Asian endemic forms. As indicated in Fig. 4, the Asian endemic taxa, anagalids, eurymylids, mimotonids, and didymoconids, account for 42% of all Shanghuan species. Although the remaining taxa show affinities to those of North America at the ordinal level, the species are not the same as those in North America. The prevalence of Asian endemic forms indicates that Asia was probably isolated from other continents during most of the Shanghuan, possibly with occasional exchanges. The occurrences of very primitive species, including *Bemalambda nanhsiungensis* (Zhou et al., 1977), *Yantanglestes conexus* (Yan and Tang, 1976; Gingerich, 1981), and *Decoredon anhuiensis* (Sza-

lay and Li, 1986), are also characteristic of the Shanghuan fauna, which suggests that Asia, especially in the south, may have been an important area for the origin of certain mammalian orders, such as the Pantodonta, Tillodontia, Arctostylopida, and Acreodi. Early migration northward from southern China very likely took place.

The composition of the Nongshanian fauna (Table 2) differs from that of the Shanghuan in several respects. The major change is the reduction of Asian endemic forms and the appearance of new taxa, including multituberculates, dinoceratans, "edentates," and arctostylopids (Fig. 5). The multituberculates and dinoceratans show a Nearctic affinity. Multituberculates have not been found in southern

China, suggesting that they probably existed only in northern Holarctica. The dinoceratans are known only from northern Asia—that is the Turfan Basin, the Ulan Nur Basin, and the Nemegt Basin—in the Nongshanian. Their occurrences in both Nongshanian and Tiffanian faunas may be considered as an indication of mammalian exchange between Asia and North America.

Asian endemic forms (Table 3, Fig. 6) are further reduced in the Gashatan. A new taxon, Rodentia, appeared. The mesonychids, arctostylopids, dinoceratans, and multituberculates increased their diversity. The shared occurrence of dinoceratans, multituberculates, tillodonts, arctostylopids, mesonychids, and rodents in both the Gashatan and the Clarkforkian indicates considerable mammalian exchange between Asia and North America. However, there is not enough evidence to indicate exchange

between Asia and Europe. The absence of multituberculates and dinoceratans from southern Chinese faunas continued through the Gashatan. This absence probably indicates environmental differences between the north and the south, especially affecting the multituberculates.

Bumbanian species are listed in Table 4. Bumbanian faunas are characterized by the appearance and increased diversity of modern mammalian orders. Insectivores, rodents, perissodactyls, primates, and carnivores comprise about half of all Bumbanian species (Fig. 7). Asian endemic forms are reduced to a small component of the total fauna. Multituberculates remain unknown in southern China. The dinoceratans had spread to the south. Basically, Bumbanian faunas are cosmopolitan and much less endemic, which indicates that the major exchange between Asia and North America had occurred.

ACKNOWLEDGMENTS

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THE LATE PALEOCENE BAYAN ULAN FAUNA OF INNER MONGOLIA, CHINA

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ABSTRACT

The history of research on the Bayan Ulan fauna is reviewed. Taxa known previously only from faunal lists and many additional taxa recovered recently are described. The Bayan Ulan fauna now comprises about two dozen taxa, including: *Lambdopsalis bulla, Prionessus lucifer, Prionessus* sp., cf. *P. lucifer, Bayanulanius tenuis, Sarcodon minor, ?Sarcodon pygmaeus, Hyracolestes* sp., cf. *Hyracolestes ermineus*, Palaeoryctoidea, incertae sedis, ?Leptictidae, n. gen. and sp., *Prolimnocyon chowi*, ?Creodonta, family indet., cf. *Viverravus* sp., *Pseudictops lophiodon, Eomylus borealis, ?Khaychina elongata, Tribosphenomys minutus, Palaeostylops iturus, Gashatostylops macrodon, Pastoralodon lacustris, Prodinoceras xinjiangensis, Pachyaena* sp., *Dissacus serratus*, and Perissodactyla, family indet. Among Mongolian Paleogene faunas, the Bayan Ulan fauna most closely resembles the Gashato, Naran, and Nomogen faunas in sharing the following taxa: *Pseudictops, Prionessus, Palaeostylops,*

Gashatostylops, Prodinoceras, Sarcodon, Hyracolestes, Pachyaena, Dissacus, and "eurymylids." These faunas are considered to form the basis for the Gashatan local land mammal age. Taxa from the Bayan Ulan fauna support biostratigraphic correlation between Gashatan faunas of Asia and those of Clarkforkian age in North America; such a correlation provides an age estimation of late Paleocene for Gashatan faunas. The absence of an arboreal faunal component in the Bayan Ulan fauna and coeval faunas indicates a relatively open habitat in the Mongolian Plateau during the early Tertiary, differing from faunas elsewhere in the same time interval and suggesting a paleozoological province distinct from those of more southerly and coastal regions of China. Mammal coprolites and probable bird pellets common at Bayan Ulan prove to be an important source not only for micromammal fossils but also for information bearing on several issues of taphonomy and paleoecology.

INTRODUCTION

The earliest Tertiary mammals from the Mongolian Plateau are generally considered to be late Paleocene in age, represented typically by the Gashatan local faunas of Mongolia. A well-known hiatus separates the late Paleocene from underlying late Cretaceous sediments and faunas that are prominent for abundant dinosaur and early mammal remains. The age determination of the Gashatan faunas has been based primarily on correlation with the Clarkforkian North American Land Mammal Age (hereafter, NALMA). The Clarkforkian NALMA, formerly deemed to straddle the Paleocene–Eocene boundary, marks the first appearance of several higher-level taxa of eutherians in the evolutionary history of mammals (Rose, 1981). A similar pattern characterizes Gashatan faunas of the Mongolian

Plateau. Biostratigraphic correlation between Gashatan and Clarkforkian faunas of the two continents is based on this similarity, although the Mongolian pattern is more subtle than that of North America.

A massive effort to improve the documentation for the early history of mammals in the Mongolian Plateau over the past several decades has resulted in the discovery of many early Tertiary faunas in the region, of which the Bayan Ulan fauna is an outstanding example. Several interesting studies have been published based on the Bayan Ulan material (Miao, 1988; Meng, 1992; Meng et al., 1994; Meng and Wyss, 1995, 1997). Although it was first reported in 1979 (Qi, 1979), the Bayan Ulan fauna as a whole has not previously been described. This absence of detailed taxonomic treatment for most

faunal elements has clouded assessments of the age of the Bayan Ulan fauna and hampered efforts to correlate the earliest Tertiary faunas of the Mongolian Plateau. This study presents a brief review of the history of research on the fauna, morphological data for most taxa recovered over the past 20 years, and some implications for faunal correlation, biogeography, taphonomy, and paleoecology. Given the limitations of space imposed by this volume and new forms promised to come from continuing preparation, this study by no means represents the definitive treatment of the subject; rather, it is our intent that the data presented here will move the study of the Bayan Ulan fauna an initial step forward.

Institutional abbreviations used in text are: AMNH, American Museum of Natural History, New York, New York; UCMP, Museum of Paleontology, University of California, Berkeley, California; UM, University of Michigan, Ann Arbor, Michigan; UW, University of Wyoming, Laramie, Wyoming; V, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, People's Republic of China.

HISTORY OF RESEARCH

In July of 1928, a field party from the Central Asiatic Expeditions (CAE) of the American Museum of Natural History visited the Nom Khong Shireh of Inner Mongolia while making its way northeast from Shara Murun to Erlian. Nom Khong Shireh (known as Nomogen today, and meaning "holy") is an isolated mesa, which stands like a huge cake in the middle of a vast basin. The expedition team established a camp, named "The Holy Mesa" (Fig. 1) by the CAE (Andrews, 1932: 400), on top of the mesa near its northern edge (Spock, 1928:field notes) on the morning of July 9. The party carried out five days of paleontological reconnaissance along the cliffs defining the mesa, leaving the area on July 14. Fossils, labelled with field numbers 773–790 (Granger, 1928:field notes), were collected from two stratigraphic levels forming the main body of the mesa; the lower of these was then regarded as pertaining to the Ulan Gochu Formation, while the upper was termed the Boron Sog Formation. No fossils were recovered at that time from the mesa's basal-extreme levels which extend several kilometers northward from its foot.

Nearly a half century later in the 1970s, Chinese geologists from the Geological Survey of Inner Mongolia mapped the Erlian (Erenhot) basin on a scale of 1:200,000. The basin extends southwest to northeast within the latitude and longitude coordinates of 42°–44°N and 110°–114°E (Fig. 1); most of the region lies within the Ulanchabu Meng (District) of the Nei Mongol (Inner Mongolia) Autonomous Region. Fossil localities within the basin include the Tunggur area at its eastern end and the Shara Murun area to the west. Given the central role that vertebrate fossils play in determining Tertiary stratigraphy in this area, paleontologists from the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, were invited to work with the mapping team during several mapping seasons. This collaborative effort resulted in the discovery of several new fossil localities in the vicinity of the Nomogen mesa, two of which are discussed below.

The first of the new fossiliferous localities brought to light by these renewed mapping activities occurs within the Nomogen Formation, at its type section near Haliut, approximately 55 km south of the Holy Mesa. This formation was first published by Chow (Zhou) et al. (1976), who noted its earlier use by the Geological Survey of Inner Mongolia mapping team. The Chow et al. study refers to three fossiliferous sites: Haliut, Gonghudong, and Tabutaonegai. Haliut, located 3 km (reported as 6 km by Russell and Zhai [1987]) southeast of what was once the Nomogen Commune (Fig. 1), is the type locality of the Nomogen Formation. Here the formation consists of three levels measuring approximately 16 m in aggregate thickness (reported as 14 m by Russell and Zhai [1987]). At Gonghudong, 3 km (4 km in Russell and Zhai [1987]) south of the former Nomogen Commune, a southwestern extension of the Nomogen Formation is reported to be exposed (Chow et al., 1976). Although detailed stratigraphic and sedimentological information for this site was not provided, these deposits were judged to be similar lithologically to those of Haliut (Chow et al., 1976). At Tabutaonegai, 4 km east of Haliut, five stratigraphic levels have been recognized (Chow et al., 1976:fig. 2). Of these five levels, only the lowest—which underlies light-colored fluvial Eocene sediments yielding *Lophialetes*—is considered referable to the Nomogen Formation. This basal stratigraphic level at Tabutaonegai was believed to be correlative with the two lower units
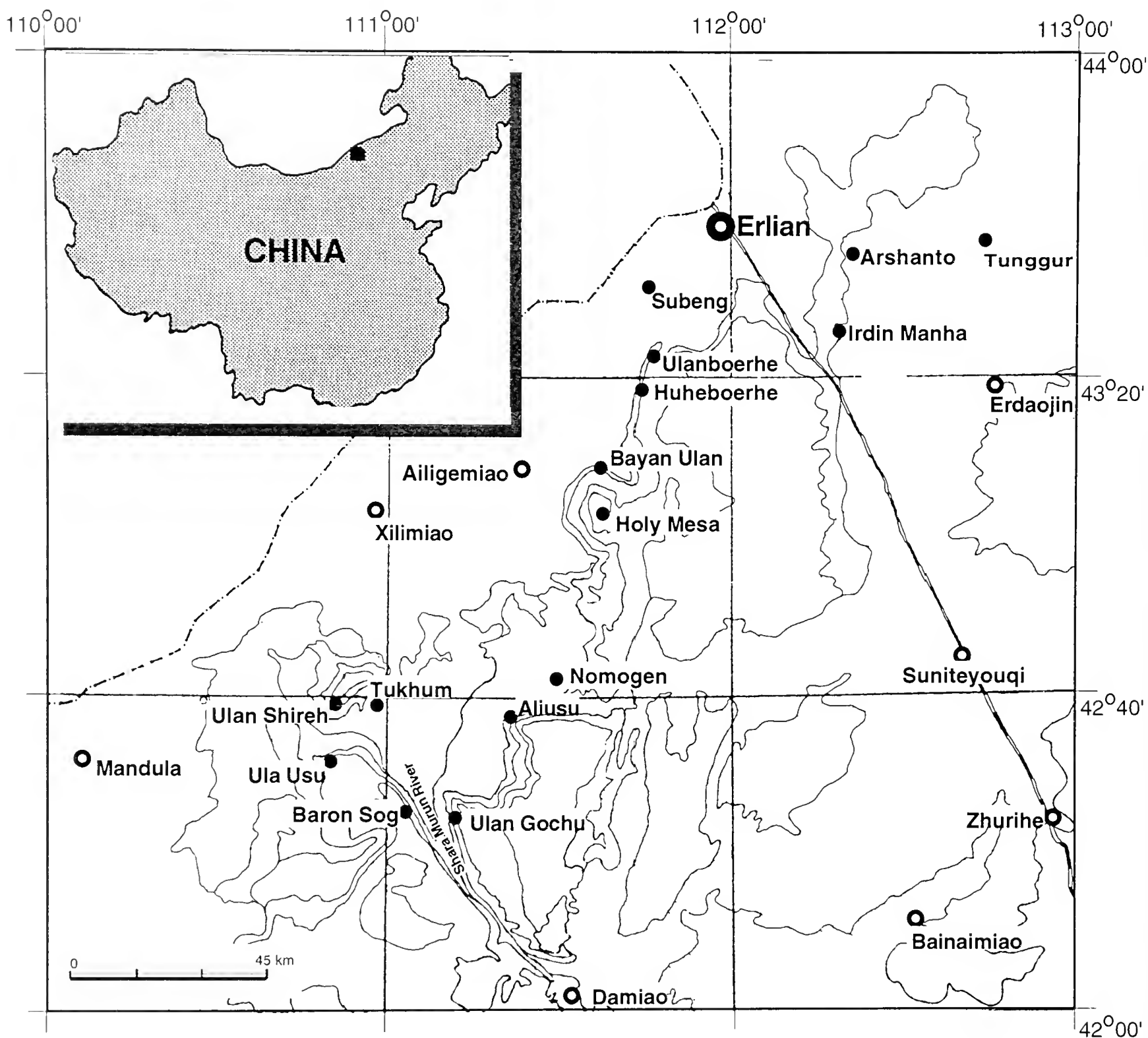
Fig. 1.—Locality map of the Erlian Basin (after Jiang, 1983).

at Haliut (Chow et al., 1976:229). Chow et al. (1976) provided a provisional taxonomic listing for the Nomogen fauna, with a fuller description of the taxa, collected primarily from Haliut and Gonghudong, appearing shortly thereafter (Chow and Qi, 1978). The fauna derived therefrom is considered late Paleocene in age, the first late Paleocene fauna known from northern China.

Although not mentioned in the original papers (Chow et al., 1976; Chow and Qi, 1978), "the fossils were found in pits that had been dug by miners in search of celestite" (Russell and Zhai, 1987:52). *Palaeostylops* and *Lambdopsalis* are by far the fauna's commonest elements (Chow et al., 1976; Chow and Qi, 1978; Jiang, 1983). By the time one of us

(J.M.) visited the Haliut area in 1992, mining operations had ceased, and we are unaware of any recent recovery of fossils from this area.

The second major locality discovered during the last two decades is from Bayan Ulan at the northern foot of the Holy Mesa (Fig. 1), where reddish clays extend for several kilometers, forming badlands of rather low relief. This area is called Bayan Ulan (meaning rich red) by the local people because of the vivid color of its sediments. Qi (1979) formally recognized the Bayan Ulan fauna for a fossil assemblage derived from this area. Along with coining names for several other new biostratigraphic and lithostratigraphic units in the area, Qi assigned these fossiliferous strata to the "Bayan Ulan Formation,"

a name first used by the geological mapping team (see also Jiang, 1983:fig. 2). Qi's listing of mammalian taxa from Bayan Ulan did not include detailed stratigraphic information or descriptions of the fossils. In addressing the general stratigraphic context, however, Qi suggested that at Bayan Ulan the "Bayan Ulan Formation" is continuous with the underlying Nomogen Formation. Further, Qi observed that most species from the Bayan Ulan and Nomogen formations are the same, excepting the occurrence of ?*Lambdotherium* sp. and ?*Heptodon* sp. at Bayan Ulan. While favoring early Eocene and late Paleocene ages for the Bayan Ulan and Nomogen formations respectively, Qi entertained two additional possibilities—that both are either late Paleocene or early Eocene in age. In describing mammals from "Huhebolhe," a cliff northeast of Bayan Ulan, Qi (1980) again suggested an early Eocene age for the "Bayan Ulan Formation."

The first description of the "Bayan Ulan Formation" at the Bayan Ulan locality occurs in the summary of the 1:200,000 mapping study on the early Tertiary in the Erlian Basin (Jiang, 1983). Several new names were proposed for newly discovered rock units and for replacement of those employed by the CAE (Fig. 2). One of these new names, the "Bayan Ulan Formation," and the lithostratigraphic unit to which it is assigned, are central to Jiang's treatment. Jiang (1983:27) stated: "The Bayan Ulan Formation was established by our team. It is best represented by the section at the Bayan Ulan area . . . . Establishment of this formation is based on presence of *Mongolotherium*, ?*Lambdotherium* sp., and ?*Heptodon* sp. . . . in the Bayan Ulan section, the Bayan Ulan Formation and Nomogen Formation are continuous; both are brown reddish lake sediments . . ." (original in Chinese). Thus it would seem that lithologic distinctiveness played little role in recognition of this new rock unit. In providing the stratigraphic section for the "Bayan Ulan Formation" at Bayan Ulan, Jiang described an additional section of the same formation from U-lan-bo-er-he (= "Huhebolhe" of Qi, 1980), a cliff northeast of the Holy Mesa (Fig. 1).

Various names have been cited in the literature for sites on this cliff, so that some clarification is in order here. On Jiang's geological map (1983:fig. 2) the names of two localities, U-lan-bo-er-he and Hu-he-bo-er-he, appear (in Chinese) near a cliff about 30 km northeast of the Holy Mesa, the latter name being placed slightly south of the former (Fig. 1). This area corresponds roughly to the "Camp Margetts area" referred to by the CAE (see

Meng, 1990). Russell and Zhai (1987:fig. 28) used the spellings Ulanborho and Fuhoborho for the same areas indicated by Jiang. Following his usage of the name "Huhebolhe," Qi (1987) later used "Huhe Bulak" to indicate the same area, and still later employed "Ulanblak" and "Huheblak" for U-lan-bo-er-he and Hu-he-bo-er-he, respectively (Qi, 1990). Meng (1990), in attempting to resolve this conflicting usage of names, spelled Hu-he-bo-er-he as Huhoborho. In the interest of simplicity it seems best to replace these "Pinyinenglish" spellings with the official Pinyin in translating the Chinese names published by Jiang (1983) into "English," that is, U-lan-bo-er-he and Hu-he-bo-er-he, or Ulanboerhe and Huheboerhe, the later locality being a few kilometers south of the former on the same cliff.

In an unpublished manuscript dated 1983, Zhai briefly described the Bayan Ulan fauna and discussed its implications for the "Gashatan" Provincial Land Mammal Age. That stalled effort served as the starting point for the present contribution. Zhai concluded that the Bayan Ulan and Gashato faunas were likely early Eocene rather than late Paleocene, a possibility suggested earlier (with regard to the latter fauna) by Szalay and McKenna (1971). Li and Ting (1983:appendix IV) went further in proposing the Bayanulanian as a "Chinese Provincial [Mammalian] Age," spanning the Paleocene–Eocene boundary. In their text (Li and Ting, 1983:22), however, these authors regarded the "Bayan Ulan Formation" and its fauna as early Eocene in age, and did not consider the Nomogen Formation as the basal part of the Bayan Ulan section.

Qi's (1987) analysis of the middle Eocene Arshanto fauna treated several stratigraphic issues concerning the early Tertiary of Inner Mongolia, the "Bayan Ulan Formation" among them. Qi concluded that the CAE's "Arshanto Formation" is divisible into three units, the late Paleocene Nomogen beds, the early Eocene Bayan Ulan beds, and the middle Eocene Arshanto beds. Qi grouped the Nomogen and Bayan Ulan beds into the Nomogen Formation, whereas the Arshanto beds and overlying Irdin Manha beds were associated in the Irdin Manha Formation (Fig. 2; but see Meng, 1990). Thus, as a lithostratigraphic term "Bayan Ulan" is no longer accorded formational status (Qi, 1987; BGMRNMAR, 1991).

Qi's (1987) analysis also includes the first English descriptions of stratigraphic sections for Bayan Ulan and Huheboerhe (= Huhe Bulak). A comparison of the stratigraphic sections published by Qi
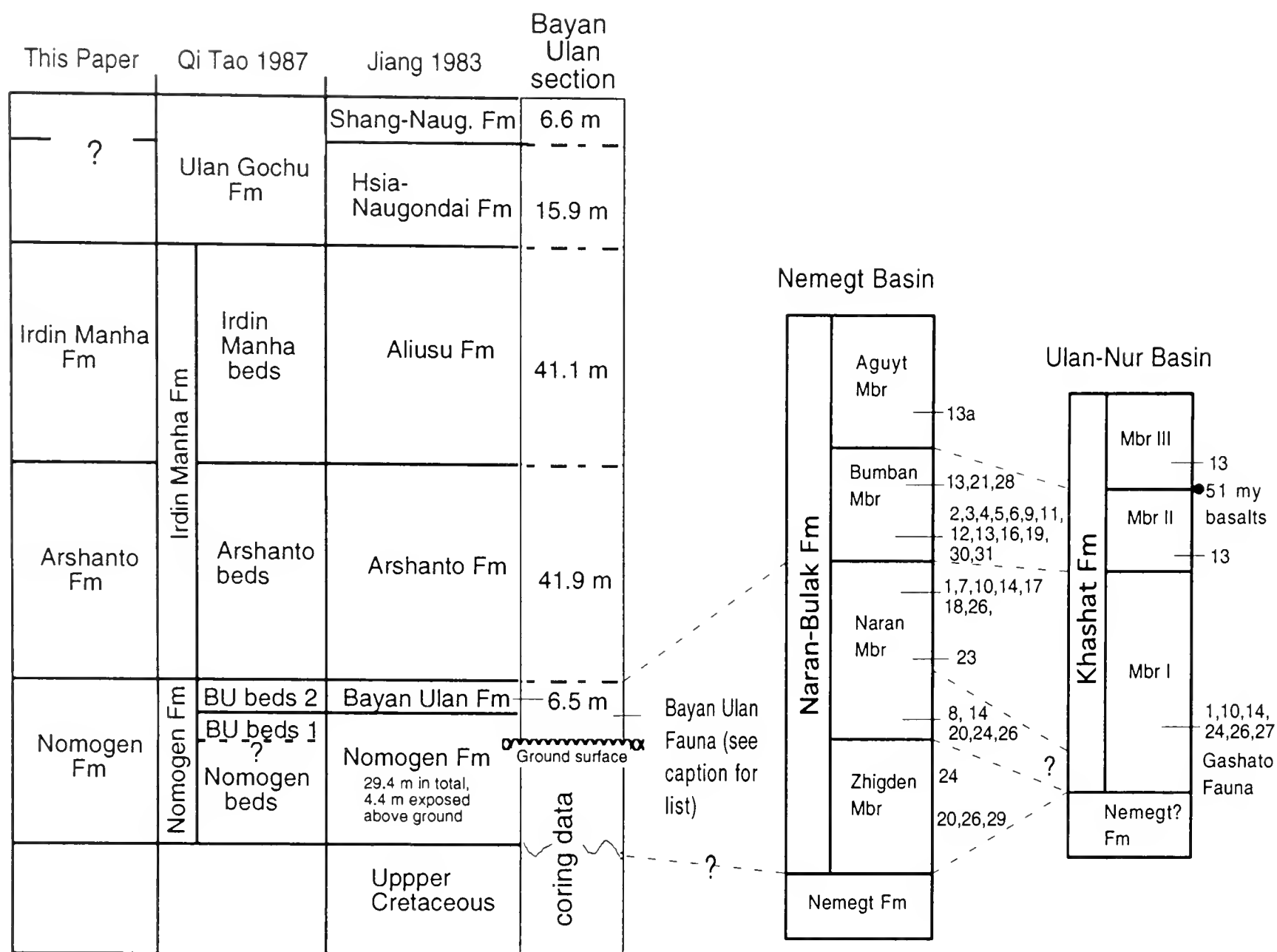
This Paper	Qi Tao 1987	Jiang 1983	Bayan Ulan section
?	Ulan Gochu Fm	Shang-Naug. Fm	6.6 m
		Hsia-Naugondai Fm	15.9 m
Irdin Manha Fm	Irdin Manha beds	Aliusu Fm	41.1 m
Arshanto Fm	Arshanto beds	Arshanto Fm	41.9 m
Nomogen Fm	BU beds 2	Bayan Ulan Fm	6.5 m
	BU beds 1 ?	Nomogen Fm 29.4 m in total, 4.4 m exposed above ground	Ground surface
	Nomogen beds	Uppper Cretaceous	coring data

(Irdin Manha Fm label runs vertically in Qi Tao column; Nomogen Fm label runs vertically)

Bayan Ulan Fauna (see caption for list)

?

Nemegt Basin

Naran-Bulak Fm		
	Aguyt Mbr	13a
	Bumban Mbr	13,21,28
		2,3,4,5,6,9,11,12,13,16,19,30,31
	Naran Mbr	1,7,10,14,17 18,26,
		23
	Zhigden Mbr	8, 14 / 20,24,26
		24
		20,26,29
	Nemegt Fm	

Ulan-Nur Basin

Khashat Fm		
	Mbr III	13
		51 my basalts
	Mbr II	13
	Mbr I	1,10,14,24,26,27 Gashato Fauna
	Nemegt? Fm	?

Fig. 2.—Division and correlation of the Bayan Ulan section (after Jiang, 1983; Qi, 1987; and Dashzeveg, 1988). The Bayan Ulan fauna consists of *Lambdopsalis bulla*, *Prionessus lucifer*, *Prionessus* sp., cf. *P. lucifer*, *Bayanulanius tenuis*, *Sarcodon minor*, ?*Sarcodon pygmaeus*, *Hyracolestes* sp., cf. *H. ermineus*, Palaeoryctoidea, incertae sedis, ?Leptictidae, n. gen. and sp., *Prolimnocyon chowi*, ?Creodonta, family indet., cf. *Viverravus* sp., *Pseudictops lophiodon*, *Eomylus borealis*, ?*Khaychina elongata*, *Tribosphenomys minutus*, *Palaeostylops iturus*, *Gashatostylops macrodon*, *Pastoralodon lacustris*, *Prodinoceras xinjiangensis*, *Pachyaena* sp., *Dissacus serratus*, and Perissodactyla, family indet.

To compare with the Bayan Ulan fauna, faunal elements from Gashato and Naran Bulak are cited below from Dashzeveg (1988): 1, *Prionessus lucifer*; 2, *Naranius infrequens*; 3, *Bumbanius rarus*; 4, *Oedolius perexiguus*; 5, *Tsaganius ambiguus*; 6, *Hyopsodus orientalis*; 7, *Dissacus indigenus*; 8, *Pachyaena nemegetica*; 9, *Hapalodectes* sp.; 10, *Eurymylus laticeps*; 11, *Zagmys insolitus*; 12, *Rhombomylus* sp.; 13, *Gomphos elkema*; 13a, *Gomphos* sp.; 14, *Pseudictops lophiodon*; 15, Mixodontia nov.; 16, Rodentia (*Sharomys singularis*, *Sharomys parvus*, *Kharomys mirandus*, *Kharomys gracilis*, *Tsaganys subitus*, *Ulanomys mirificus*, *Boromys grandis*, *Alagomys inopinatus*, *Orogomys obscurus* [see Dashzeveg, 1990a, 1990b]); 17, *Oxyaena* sp.; 18, "*Sinopa*" sp.; 19, *Altanius orlovi*; 20, *Archaeolambda planicanina*; 21, *Archaeolambda* sp.; 22, *Archaeolambda trofimovi*; 23, *Coryphodon tsaganensis*; 24, *Prodinoceras martyr*; 25, *Pridinoceras* sp.; 26, *Gashatostylops* (= *Arctostylops*) *macrodon*; 27, *Palaeostylops* (= *Arctostylops*) *iturus*; 28, *Palaeostylops* (= *Arctostylops*) sp.; 29, *Ernanodon* sp.; 30, *Hyracotherium gabuniai*; 31, *Homogalax namadicus* (elements 15, 22, and 25 from the Bugin Member at the Bugin Tsav Basin).

and by Jiang reveals substantial differences. Qi identifies the lowest levels of the two stratigraphic columns as belonging to the early Eocene Bayan Ulan beds of the Nomogen Formation, while in Jiang's columns these levels are attributed to different formations (the Nomogen Formation below and "Bayan Ulan Formation" above) in both sections. Inasmuch as Qi's (1987:8) Bayan Ulan section is cited as being based on the work of the Inner Mon-

golian mapping team, the dissimilarities between Jiang's and Qi's sections would appear to stem from differences in field interpretation. Whatever the source of this disagreement for the Bayan Ulan section, however, it appears that level 1 of the Bayan Ulan beds of the Nomogen Formation in Qi's usage is equivalent to the upper part of the Nomogen Formation of Jiang's usage and that level 2 of the Bayan Ulan beds of the Nomogen Formation in Qi's

usage is equivalent to Jiang's "Bayan Ulan Formation" (Fig. 2).

These authors' section descriptions for the Ulanboerhe area are also at variance lithologically and paleontologically, perhaps due to measurements along different transects through the same cliff. For instance, among several peculiar occurrences of fossils, we note that tapirs were reported for the Bayan Ulan beds from the Ulanboerhe section in one study (= Huhe Bulak; Qi, 1987:8) but not in the other (Jiang, 1983), whereas Hyopsodontidae were cited as occurring in the Nomogen Formation by Jiang but not by Qi. Given published descriptions, we are unable to reconcile these two conflicting accounts. To avoid confusion, we describe below only fossils from Bayan Ulan itself.

In their review of the Paleogene of Asia, Russell and Zhai (1987) referred (with a query) the Bayan Ulan fauna to the Nomogen Formation, regarding it as transitional Paleocene–Eocene in age. Accordingly, this fauna was included in neither the late Paleocene "Nongshanian" nor the early Eocene "Bumbanian" Land Mammal Ages of Asia (the Gashato, Nomogen, Zhigden, and Naran faunas making up the former) (Russell and Zhai, 1987). The Bayan Ulan fauna has recently been considered to be latest Paleocene in age (Ting, 1995, 1998) based on the first appearance of the order Rodentia, represented by *Tribosphenomys*.

Although taxonomic lists for the Bayan Ulan fauna have circulated for over 15 years, the fauna as a whole has not previously been formally described. Only one taxon from this fauna, *Lambdopsalis bulla*, has been thoroughly studied (Miao,

1986, 1988). Since Russell and Zhai's (1987) compilation, additional collecting at Bayan Ulan, primarily by Meng and Wyss during field seasons in 1987 and 1992–1995, has yielded several new taxa and new material of taxa previously known, some of which have been published (e.g., Meng, 1992; Meng and Wyss, 1994, 1995, 1997; Meng et al., 1994). The importance of this accumulated material makes description of the fauna as a whole all the more urgent.

Taxa new to the Bayan Ulan fauna described herein are all small-bodied forms, most of which have been recovered from calcium carbonate cemented nodules (likely representing carnivorous mammal coprolites and fossil raptorial bird pellets) via acid preparation (Meng and Wyss, 1996, 1997). With this newly recognized source of Bayan Ulan micromammals, the number of species known from Bayan Ulan has doubled since the most recent tabulation (Russell and Zhai, 1987). Numerous unprocessed nodules remain on hand, promising that preparation over the coming years will lengthen this taxonomic list even further. Not only has the new material yielded phylogenetically important information for several major mammalian clades, such as Glires and Multituberculata (Meng et al., 1994; Meng and Wyss, 1995), it has also enhanced the fauna's biostratigraphic, paleogeographic, and taphonomic utility. Our intention here is to provide the long overdue taxonomic treatment of the Bayan Ulan fauna—not wishing to delay this process even further awaiting completion of preparation—with the hope that more thorough treatments of several aspects of the fauna will be forthcoming.

OCCURRENCE OF FOSSILS

The stratigraphic sequence exposed at Bayan Ulan debatably constitutes five or six rock units that measure about 110 m in total thickness (Jiang, 1983; Fig. 2). Exposures of these beds extend over 5 km in a flat area, and only the younger beds rise to form the Holy Mesa. Division and correlation of this sequence have been inconclusive (Jiang, 1983; Qi, 1987; Russell and Zhai, 1987; Meng, 1990). According to Jiang (1983), the basal part of the section is divided into two units, the most basal 4.4 m red beds and the overlying 6.5 m red beds—the former is believed to be the exposed portion of the Nomogen Formation, whereas the latter represents the entire "Bayan Ulan Formation." Coring reveals that there are 25 m of unexposed sediments belonging

to the Nomogen Formation in this region (Fig. 2). One of the problems that has hampered study of the Bayan Ulan fauna for years is whether there are two faunas, namely the Nomogen fauna and Bayan Ulan fauna, from the two basal beds, respectively. Jiang (1983) believed there were two: one from the most basal 4.4 m red beds and the other from the overlying 6.5 m red beds. Fossils attributed to the basal 4.4 m red beds are *Prionessus lucifer*, *Sarcodon pygmaeus*, *Palaeostylops iturus*, and Archaeolambdidae (n. gen. and sp.); those from the 6.5 m overlying beds include *Prionessus lucifer*, *Mimotona borealis* (= *Eomylus borealis*), *Palaeostylops iturus*, *Palaeostylops macrodon* (= *Gashatostylops macrodon*), *Pseudictops lophiodon*, *Pastoralodon*

lacustris, Plagiocristodon serratus, Pachyaena sp., *Pyrodon* sp. (= *Prodinoceras*), *Mongolotherium efremovi* (= *Mongolotherium xinjiangensis*), *Mongolotherium* sp. (= *Prodinoceras*), ?*Lambdotherium* sp., and ?*Heptodon.*

As pointed out above, however, the "Bayan Ulan Formation" was proposed for the overlying 6.5 m red beds based on the presence therein of *Mongolotherium,* ?*Lambdotherium* sp., and ?*Heptodon* sp., not on lithological evidence. Therefore, the designation of "Bayan Ulan Formation" has been abandoned (Qi, 1987; BGMRNMAR, 1991) because of insufficiency of lithological evidence, although this reasoning has never been spelled out explicitly. Still, Qi (1987:4–5) considered that the Nomogen Formation "contains two levels: the upper Lower Eocene Bayan Ulan beds and the lower Upper Paleocene Nomogen beds (or celestite-nodule bearing beds)," and regards the 4.4 m red beds and the 6.5 m red beds as levels 1 and 2 of the "Lower Eocene Bayan Ulan beds" of the Nomogen Formation. This highlights the problem regarding the relationship between the "Bayan Ulan beds" at Bayan Ulan and the original type Nomogen Formation at Haliut. It appears that Qi regarded the original Nomogen Formation as the "Nomogen beds," which are supposed to underlie the "Bayan Ulan beds." Because of the exclusive exposure of the "Bayan Ulan beds" at Bayan Ulan and their absence at the type locality of the Nomogen Formation, the supposed superpositional relationship of the "Nomogen beds" and "Bayan Ulan beds" is supported by no observable sequence. This leaves open the possibility that the "Nomogen beds" at Haliut and the "Bayan Ulan beds" at Bayan Ulan are correlative; in other words, the sediments exposed at Haliut, given the contained celestite nodules, may represent a facies variation of the "Bayan Ulan beds" at Bayan Ulan. Tracing these beds laterally over a distance of 55 km in the field is precluded by incomplete exposure. As noted by Jiang (1983), however, the fossil composition of the Nomogen Formation is characterized by a high percentage—more than 90% of the total— of specimens of *Lambdopsalis* and *Palaeostylops.* A similar percentage is documented in the Bayan Ulan beds. This unusual faunal proportion may be cited as biostratigraphic evidence indicating that the "Bayan Ulan beds" and the "Nomogen beds" are stratigraphically equivalent. Therefore, until superpositional evidence becomes available, we prefer to consider the basal beds (the 4.4 m plus the 6.5 m red beds) at Bayan Ulan as the lateral extension of the Nomogen Formation. The terms "Nomogen beds," "Bayan Ulan beds," and "Bayan Ulan Formation" will not be used in this paper (Fig. 2). Qi's levels 1 and 2 in his "Bayan Ulan beds" at Bayan Ulan are referred to as levels 1 and 2 in the Nomogen Formation at Bayan Ulan.

Now the question arises as to whether it is necessary, or even possible, to divide the fossils from the Nomogen Formation at Bayan Ulan into two assemblages. We believe it is unnecessary. The main fossiliferous sites we worked occur as two patches of exposure, separated by about 200 m but at the same stratigraphic level. The western patch produces abundant specimens of *Lambdopsalis* with sparse *Palaeostylops,* while in the eastern patch, *Palaeostylops* is more common. With careful investigations in several seasons, we were unable to discern any distinct boundary for two faunal assemblages. It appears that current evidence precludes reliable subdivision of the fossil assemblage and therefore we regard all fossils from the basal red beds (11 m thick) as one Bayan Ulan fauna.

Another problem confronting us is the possibility of mixing fossils from early collections from various faunal levels and localities. For the Bayan Ulan locality, which is topographically flat, it seems unlikely that fossils from the overlying Arshanto Formation have been transported to the basal beds yielding the Bayan Ulan fauna, although a small chance for such mixing cannot be excluded. It is possible, however, that specimens were accidently mixed with the Bayan Ulan fauna by investigators working at various localities. To minimize the possibility of faunal mixing, our field collecting during five seasons was purposely restricted to the basal beds. In this manner, we attempted to confirm occurrences of fossils previously reported from this region. We have collected all taxa listed in Russell and Zhai (1987) except *Pachyaena* and the questionable ?*Heptodon* sp. and ?*Lambdotherium* sp. ?*Heptodon* sp., represented by half of an upper molar that shows advanced features, is likely to be from younger beds or even from other localities; therefore, we exclude this species from the Bayan Ulan faunal list. We retain *Pachyaena* and the questionable perissodactyl taxon in the fauna, with the expectation that future investigations will corroborate their occurrence in these deposits. With the exception of these two taxa, we are confident that all the taxa described below are derived from the basal beds measuring about 10 m in thickness at Bayan Ulan. In addition to fossil mammals, fragments of other vertebrate groups were found at Bayan Ulan, including a vertebra of a lizard, possibly belonging

to Varanidae, a distal tarsometatarsus of a bird, and five vertebrae of *Amia*.

Finally, we caution against the referral of fossil assemblages from other localities to the Bayan Ulan fauna. In this study, the designation "Bayan Ulan fauna" refers strictly to the fossil assemblage derived from the basal beds (the upper Nomogen Formation) at the Bayan Ulan locality (Fig. 2). Other fossil assemblages recovered in this vicinity are better correlated with it, rather than included in it.

SYSTEMATIC PALEONTOLOGY

Multituberculata Cope, 1884
Taeniolabidoidea Sloan and Van Valen, 1965
Lambdopsalis bulla Chow and Qi, 1978

Comments.—*Lambdopsalis bulla* was named on the basis of specimens from the Nomogen locality (Chow and Qi, 1978). This taxon has been thoroughly studied by Miao (1986, 1988), whose monographic treatment includes material from both the Nomogen and Bayan Ulan localities. Additional studies on the ear region and postcranials have been carried out by several workers (Miao and Lillegraven, 1986; Miao, 1988; Kielan-Jaworowska and Qi, 1990; Meng, 1992; Meng and Miao, 1992; Meng and Wyss, 1995). Given these extensive descriptions and reviews, further consideration of this taxon is unnecessary here. *Lambdopsalis bulla* is the most common element of the fauna and the best studied taxon from Bayan Ulan, but it is somewhat paradoxical that this taxon has not previously been mentioned in any published faunal lists (Qi, 1979, 1987; Jiang, 1983; Li and Ting, 1983; Russell and Zhai, 1987).

Prionessus Matthew and Granger, 1925

Revised Diagnosis.—Small taeniolabidoid multituberculate; tooth formula 2–0–1–2/1–0–1–2; lower incisor oval in cross section, with enamel covering labial side and root extending under M_2; P_4 unicuspid and single- or double-rooted; M_1 cusp formula 5:4 and M_2 3:2 or 4:2; I^2 enamel restricted to labial side; I^3 single-cusped and positioned at the labial margin of palate, lateral to the posterior end of the elongate, medium-sized incisive foramen; P^3 single-cusped, with one or two roots; M^1 cusp formula 6–7:7–8:4–5 and M^2 1:2:3; single infraorbital foramen dorsal to P^4, opening anterolaterally; nasal with expanded posterior half but lacking contact with parietal; frontal–parietal suture V-shaped; posterior border of palate medial to the middle of M^2; and angular process inflected. Differing from *Sphenopsalis* and *Lambdopsalis* in being much smaller.

Comments.—Three multituberculate genera from the early Tertiary of the Mongolian Plateau have been described: *Prionessus*, *Lambdopsalis*, and *Sphenopsalis*. On the basis of ten dental characters, *Prionessus* was postulated as the nearest outgroup of *Lambdopsalis*, with the caveat that five of the ten features in *Sphenopsalis* cannot be scored (Miao, 1986). Nonetheless, this relationship was upheld by an analysis involving more taxa (Simmons and Miao, 1986). In the most recent treatment of multituberculate phylogeny (Simmons, 1993), *Prionessus* and *Sphenopsalis* are not included. The revised diagnosis of *Prionessus* provided above suggests that polarities of a few characters have been inconsistently presented in previous studies, stemming partly from their differing levels of generality (Simmons, personal communication). Two features relevant to *Prionessus* are the position of I^3 and the number of P_4 roots. An I^3 placed near the labial edge of the premaxilla has been regarded as a primitive condition, contrasting with a more medial position (Miao, 1986:character 4). This polarity is reversed in Simmons and Miao (1986) and then reversed again in Simmons (1993:character 22). Following the latest study by Simmons, the marginal placement of I^3 in *Prionessus* is here considered the primitive condition for the Mongolian Tertiary taxa. Miao (1986:character 3) considered the double-rooted condition in both P^4 and P_4 to be primitive, while the same polarity is retained only for P^4 in other studies. A single-rooted P^4 has previously been regarded as diagnostic of *Prionessus*, a characterization partly contradicted by the new material described below. Some specimens of *Prionessus* show a double-rooted condition in both P^4 and P_4, a character generally held to be primitive for multituberculates (Clemens and Kielan-Jaworowska, 1979; Miao, 1986; Simmons and Miao, 1986; Simmons, 1993). According to Simmons (1993), several other features of *Prionessus* can also be considered more primitive than those of *Lambdopsalis* and *Sphenopsalis*, including fewer cusps on M^1, posterior border of palate medial to the middle of M^2, and nasal lacking contact with parietal.

Prionessus lucifer Matthew and Granger, 1925
(Fig. 3a)

Referred Specimens.—V11131.1, a partial skull with left M^1 and erupting left and right M^2;
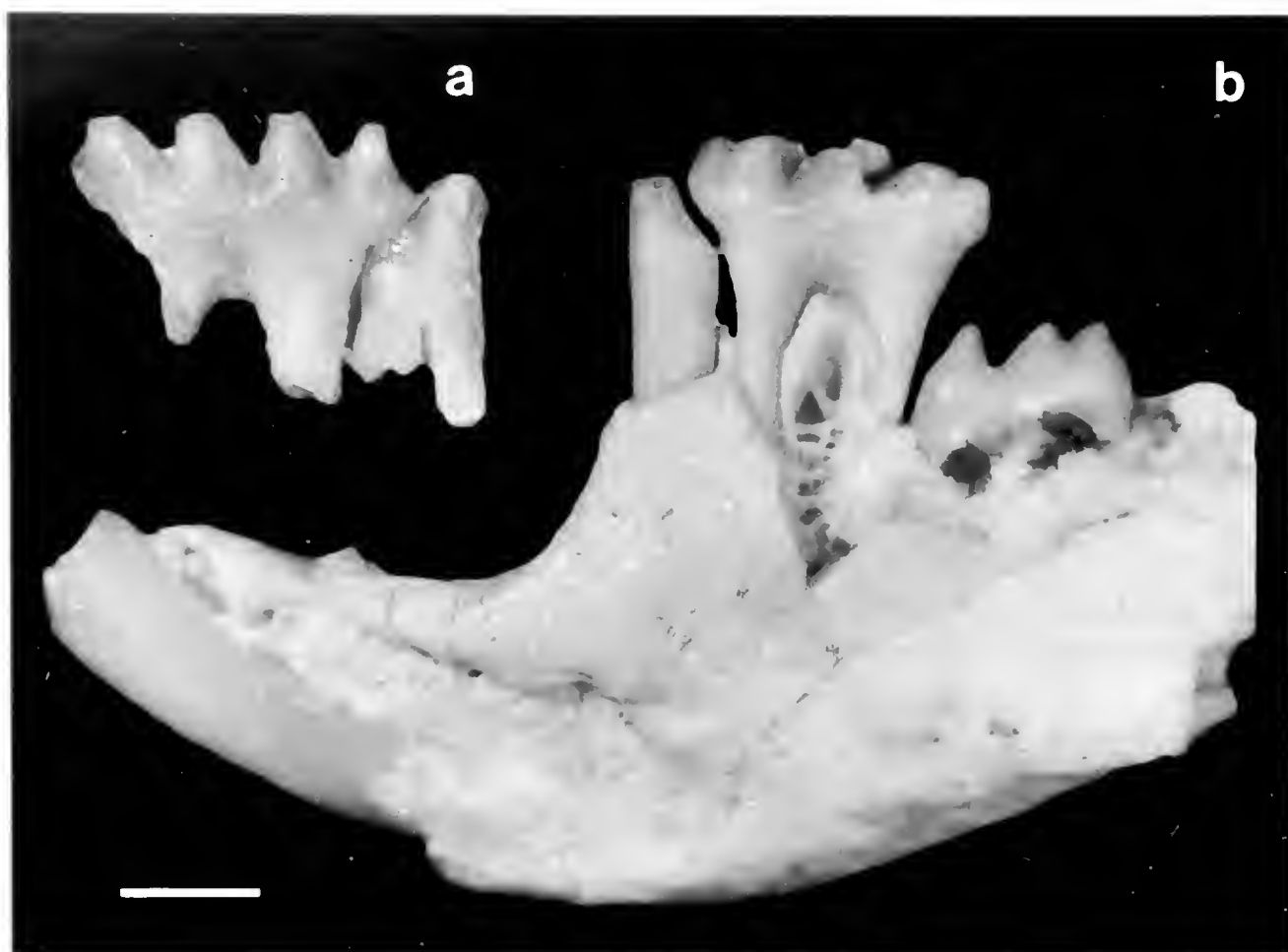
Fig. 3.—Lower dentitions of *Prionessus*. a. Lingual view of left P_4–M_1 (V11131.2), showing the double-rooted P_4 of *Prionessus lucifer*. b. Labial view of a left mandible (V11132) bearing a single-rooted P_4, attributed to *Prionessus* sp., cf. *P. lucifer*. Scale = 2 mm.

V11131.2, a partial skull with root of left I^2, I^3, and P^4–M^2 on both sides, and associated left P_4–M_1 (Fig. 3a); V11131.3, a maxilla with left I^2, P^4 on both sides, and associated lower molars; V11131.4, a pair of lower jaws with incisors and molars; and AMNH 20423 (holotype), an edentulous lower jaw. AMNH 21710 and 21724, in which premolars are not preserved, are questionably referred to this species.

Description.—All referred AMNH specimens were described by Matthew et al. (1928), and little additional morphology needs to be added. Specimens from Bayan Ulan compare closely with those from Gashato (Matthew et al., 1928) and Nomogen (Chow and Qi, 1978) in size and morphology. The dental formula is 2–0–1–2/1–0–1–2. The double-rooted P_4 is unicuspid, transversely compressed, and is lower than the anteriormost cusp of M_1 (Fig. 3a). The M_1, narrower than M_2, has a 5:4 cusp formula and a small posterior cusp on the labial row. The M_2 bears three labial and two lingual cusps—similar to AMNH 21731 from Gashato but differing from specimens from the Nomogen Formation at Haliut, in which M_2 has four labial cusps (Chow and Qi, 1978).

I^2 is much larger than the simple I^3, extending posteriorly within the premaxilla to the level of the anterior opening of the infraorbital canal. I^3 occurs at the labial edge of the premaxilla, immediately lateral to the posterior end of the incisive foramen. A diastema measuring 5.5 mm occurs between I^3 and P^4. P^4 has two roots and a single-cusped, transversely compressed crown. The anterior root of P^4 is more robust than the posterior; the tooth leans slightly posteriorly. The relationship between P^4 and M^1 is obscured by fractures in the maxilla in V11131.2, but the teeth are closely spaced in V11131.1. M^{1-2}, although displaced,

are preserved on both sides of the skull (V11131.2). The M^1 cusp formula is 6–7:7–8:4. The ridge anterior to the anterior cusp on the lingual row is weak. M^2 bears a small labial cusp, two large medial cusps, and three conical lingual cusps, yielding a cusp formula of 1:2:3.

Comments.—*Prionessus lucifer* was proposed by Matthew and Granger (1925) based on an edentulous mandible from Gashato (AMNH 20423). The P_4 alveolus of the jaw shows two connate roots. More nearly complete material, including lower and upper molars collected in 1925, was partly described by Matthew et al. (1928). Undescribed material includes a mandible bearing P_4, M_1, and erupting M_2 (AMNH 21731), which was nonetheless labelled as the topotype. The P_4 in this mandible is single-rooted, differing from the type of *Prionessus lucifer*. In the maxilla referred to *Prionessus lucifer* (AMNH 21717) (Matthew et al., 1928:fig. 2), P^4 is broken but "there is a single premolar root immediately anterior to M^1" (Matthew et al., 1928:1). Reexamining the specimen, we are unable to determine whether the single premolar alveolus of AMNH 21717 housed the sole root of P^4 or whether it simply represents the posterior root of a double-rooted P^4, due to breakage of the maxilla anterior to the preserved alveolus. The new Bayan Ulan specimen (V11131.2) demonstrates that, in an individual in which both the upper and lower teeth

are preserved, both P^4 and P_4 are double-rooted. On the other hand, however, specimens with single-rooted P_4 were also discovered. We tentatively refer those specimens from Gashato and Bayan Ulan having double-rooted P_4^4 to *Prionessus lucifer*, and those with single-rooted P_4 but P^4 root condition uncertain to *Prionessus* sp., cf. *P. lucifer*, as is further discussed below.

<center>

Prionessus sp., cf. *P. lucifer* Matthew and
Granger, 1925
(Fig. 3b)

</center>

Referred Specimens.—AMNH 21731, a fragmentary mandible with P_4–M_1 and erupting M_2; V11132, a fragmentary left mandible with incisor, P_4–M_1, and erupting M_2 (Fig. 3b); and possibly AMNH 21717, a maxilla with molars on both sides.

Description.—V11132 (Fig. 3b) is similar to AMNH 21731 in having a single-rooted P_4; both are young individuals with erupting M_2. The P_4 crown in both specimens is peg-like, contrasting with the P_4 in *P. lucifer*, which is transversely compressed in crown view and triangular in lateral view. There is no indication that the P_4 is a deciduous tooth. The cusp formula of M_1 is 3:2. V11132 differs from AMNH 21731 in being slightly smaller and having slender cusps. We tentatively refer the maxilla with upper molars (AMNH 21717) to *Prionessus* sp., cf. *P. lucifer*, although this association is less than convincing for the reason discussed above.

Comments.–Prionessus sp., cf. *P. lucifer* differs from *Prionessus lucifer* mainly in having single-rooted P_4^4. Single-rooted P_4^4 are a derived feature restricted to some taeniolabidoids (Miao, 1986; Simmons and Miao, 1986; Simmons, 1993). In addition to the root condition of P_4^4, M^1 of *Prionessus* sp., cf. *P. lucifer* is smaller than that of *P. lucifer* and its M^2 is slightly larger than that of the latter. The lingual cusp row of M^1 is more anterior in *Prionessus* sp., cf. *P. lucifer* than in *P. lucifer*. Moreover, the external cusp of M^2 in *Prionessus* sp., cf. *P. lucifer* has a distinct lingual ridge extending to the anterior side of the first medial cusp and ends as a small cusp, yielding a cusp formula for M^2 of 1:3:3 (Matthew et al., 1928). In sum, *Prionessus* sp., cf. *P. lucifer* is distinguished by at least one derived feature—a single-rooted P_4. We do not know, however, whether these dental differences reflect sexual dimorphism, intraspecific variation, or distinctions between two taxa. Because P_4^4 root number is counted heavily in identifying multituberculates, it seems justifiable to separate single-rooted and double-rooted forms. Further work is needed to establish whether these two morphotypes represent distinct species. As a makeshift measure, we differentiate
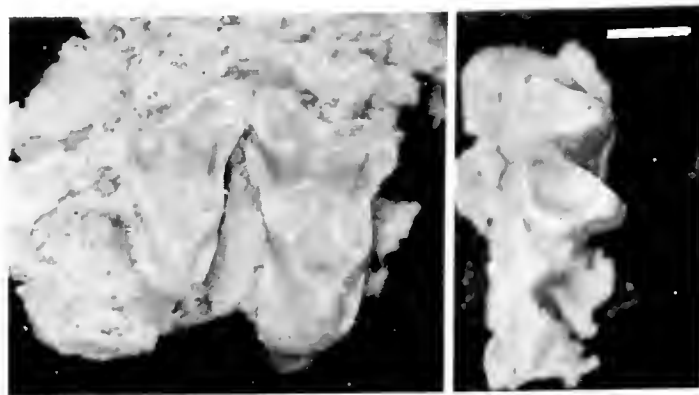
Fig. 4.—*Bayanulanius tenuis*, n. gen. and sp., holotype, V11133. Occlusal views of right M^{2-3} and right M_2. Scale = 0.5 mm.

these forms as *P. lucifer* and *Prionessus* sp., cf. *P. lucifer*, while observing that both morphotypes occur at both Gashato and Bayan Ulan.

<center>

Lipotyphla Haeckel, 1866
Soricomorpha Gregory, 1910
Nyctitheriidae Simpson, 1928
Bayanulanius, **new genus**

</center>

Type Species.—*Bayanulanius tenuis* n. sp.
Diagnosis.—As for the new species.

Etymology.—Named for the locality of Bayan Ulan.

<center>

Bayanulanius tenuis, **new species**
(Fig. 4)

</center>

Holotype.—V11133, a partial maxilla with M^{2-3} and a fragmentary lower jaw with M_2 (or M_1) (Fig. 4), derived from the same peanut-sized coprolitic nodule. These are the only known specimens and are compatible in size and morphology, probably belonging to a single individual.

Diagnosis.—Smallest of all nyctitheres with the exception of *Plagioctenoides microlestes* (Bown, 1979); differing from the latter in being more slender; molars with sharply-pointed cusps; paracone and metacone situated more closely than in other nyctitheres; conules with long and strongly ridged "wings"; M^3 considerably narrower than M^2; M_2 with an elevated cristid obliqua extending to the posterior side of the metaconid, higher in position than in other nyctitheres.

Etymology.—Latin *tenuis*, slender, indicating the slim molar structure of the species.

Description.—A crack along the lingual base of the paracone and metacone of M^2 slightly displaces this portion of the tooth; the teeth are otherwise perfectly preserved (Fig. 4). The upper molars are low-crowned and are transversely elongate. The paracone is slightly larger and higher than the metacone, the two cusps being joined at their bases by a low centrocrista. Both cusps are sharp, lingual surfaces being more vertical than the labial ones. A low preparacrista extends from the paracone anterolabially to form a moderate parastyle that is rounded in out-

line. The external shelf is narrow and bears no mesostyle. The metastyle is much stronger than the parastyle; a strong ridge extends labially from the summit of the metacone to the metastyle. A broad inclined surface is formed on the labial side of the ridge. The protocone is sharp; it aligns with and is as high as the paracone. Labially, the preprotocrista and postprotocrista are sharp, connect with the paraconule and metaconule respectively, and define a narrow trigon basin. The conules are distinct and nearly equal in size, with the paraconule more lingually placed than the metaconule. Each conule bears two sharp crests on its labial side, forming well-developed "wings." The preparaconule crista extends to the parastyle and forms the anterior edge of the tooth, while the postparaconule crista runs to the lingual base of the paracone. The premetaconule crest extends to the anterolingual base of the metacone, whereas the postmetaconule crest reaches the base of the metastyle posterolabially. These crests define two shallow, roughly triangular basins buccal to the conules: the one buccal to the paraconule is anteroposteriorly short but transversely long, whereas the one buccal to the metaconule is long but narrow. The precingulum is short and weak, butting against the anterior base of the protocone. The postcingulum is stronger than the precingulum, bearing a small hypocone at its lingual end. The cingula fail to meet at the lingual base of the protocone.

M^3 is considerably narrower and shorter than M^2. It has a very strong, anterolabially extended parastyle, slightly smaller than that on M^2; the metastyle, by contrast, is absent. The hypocone is also greatly reduced. Apart from their smaller size, other structures of M^3 compare closely to their counterparts on M^2.

The single preserved lower tooth most likely represents a M_2; it leans slightly lingually in relation to the mandible (Fig. 4). The trigonid is of moderate height and is slightly shorter anteroposteriorly and narrower than the talonid. The paraconid is reduced and crestiform; it extends lingually, terminating below the metaconid. The metaconid is as large as the protoconid. The hypoconid forms the largest cusp on the talonid; from it extends anteromedially a strong cristid obliqua. Approaching the metaconid, the cristid obliqua increases in height and merges with the metaconid posteriorly. A deep hypoflexid results from the anterolingual extension of the cristid obliqua. The cristid obliqua and the ridge connecting the hypoconid and hypoconulid demarcate a sharply angled talonid, which points labially. The hypoconulid is slightly medial to the midline of the tooth and is therefore closer to the entoconid than to the hypoconid. The entoconid is the smallest of the talonid cusps; it extends anteriorly as a high entocristid, enclosing a deep talonid basin lingually. The anterior cingulid extends from the anterior side of the paraconid to the labial base of the tooth. No external cingulid is present.

Measurements of V11133 (in mm; length, width): M^2 1.0, 1.65; M^3 0.8, 1.3; M_2 1.05, 0.62 (tal)–0.6 (tri).

Discussion.—Although appearing slightly slender, this new species is most comparable in size with the North American Wasatchian *Plagioctenoides microlestes*, of which the M_2 (UW 9667) measures 1.00 mm long and 0.75 mm wide (Bown, 1979:66). Upper molars are unknown for *P. microlestes* and the premolar is not preserved for *B. tenuis*, making comparison of these teeth impossible at present. The lower molars of *P. microlestes* differ from the M_2 of *B. tenuis* in having a lower cristid obliqua.

In general pattern, particularly in the upper teeth,

B. tenuis is closely comparable with *Leptacodon* (Matthew and Granger, 1921; McKenna, 1968; Robinson, 1968) among North American forms. These two genera appear to share several similarities: lower molars leaning slightly lingually, basined talonid, slender cusps and crests on upper and lower molars, small hypocone, narrow external shelf, large parastyle on M^3, marked conules with sharp labial crests ("wings") that surround broad basins labial to the conules, and paraconid small and crestiform. Some specimens of *Leptacodon* also show a ridged cristid obliqua. Some of these features are certainly not unique to the two taxa under consideration, such as the large parastyle on M^3 which is also present in several other taxa (McKenna, 1968). No attempt is made here to assess the polarities of these features, nor to track their distribution across an array of possible phylogenetic allies. The Bayan Ulan taxon differs from *Leptacodon* in having upper molars transversely more elongate, the paracone and metacone more closely placed, M^3 proportionally much smaller than M^2, and the hypoconulid stronger than the entoconid. These differences also apply to *Pontifactor* (West, 1974; Bown, 1979), which is further distinguishable from *B. tenuis* in having a mesostyle and a stronger hypocone on upper molars.

Among Asian forms, *Bumbanius rarus*, a nyctithere from the Bumban Member, Naran Bulak Formation of Mongolia (Russell and Dashzeveg, 1986), also shows similarities to the new species. Although damage on the M^2 (Russell and Dashzeveg, 1986: fig. 4) precludes detailed comparison, it seems that *Bumbanius rarus* has well-developed conules and "wings," although not to the degree seen in *Bayanulanius tenuis*. *Bumbanius rarus* is considerably larger, with more robust paracone and metacone situated closer to the protocone, than the new taxon. In addition, the entocristid and cristid obliqua of *Bumbanius* are less developed than in the Bayan Ulan taxon.

A second nyctithere from the Bumban Member, *Oedolius perexiguus*, is more similar in size to the new Bayan Ulan taxon than is *Bumbanius*. The upper dentition of *Oedolius* is unknown. Its lower molars have a relatively low paraconid, a more open trigonid, a labially positioned cristid obliqua, and a relatively open talonid bearing a low entocristid.

The nyctithere *Jarveia* Nessov, 1987 (Averianov, 1995) from the upper Paleocene of southern Kazakstan differs from *B. tenuis* in having more conical cusps on the lower molars, a smaller paraconid, a poorly developed crest between the protoconid and metaconid, and lack of conules on the upper molars.

Bayanulanius tenuis compares less favorably with other early North American and European "insectivores" such as *Mckennatherium, Diacodon,* and *Adunator.* These taxa are not only larger in size, but are more robust in cusp shape, suggesting perhaps erinaceomorph affinities. *Bayanulanius tenuis* differs from the possible late Cretaceous nyctithere/insectivore *Paranyctoides* (Fox, 1970, 1979, 1984) in being smaller and having anteroposteriorly compressed upper molars, better developed hypocones, and a reduced paraconid appressed against the metaconid.

A few other "insectivores" known from south and central Asia are represented by mostly fragmentary material. Two palaeoryctids from the Bumban Member, *Naranius* and *Tsaganius,* differ from the Bayan Ulan taxon mainly in having transversely more elongate upper molars with closely appressed paracone and metacone, and considerably higher trigonids on lower molars. These features also distinguish the new taxon from other early Asian "insectivores," including *Praolestes* (Matthew et al., 1929; Szalay and McKenna, 1971), *Prosarcodon* (McKenna et al., 1984), *Sinosinopa* (Qi, 1987), *Sarcodon* (Matthew and Granger, 1925; Matthew et al., 1929; Szalay and McKenna, 1971; see below). The new taxon is readily distinguished from the peculiar lipotyphlan *Carnilestes* from the Paleocene of South China (Wang and Zhai, 1995) in being much smaller, in having more slender and higher cusps on both upper and lower teeth, more closely spaced paracone and metacone, more prominent conules, and more lingually placed cristid obliqua. Although *Carnilestes* is early(?)–middle Paleocene in age, it shows numerous derived features compared to roughly contemporaneous North American lipotyphlans such as *Leptacodon* (Wang and Zhai, 1995).

Insectivora incertae sedis
Sarcodon Matthew and Granger, 1925
Sarcodon minor, **new species**
(Fig. 5)

Holotype.—V11134.1, a left M^1 (Fig. 5b, d).

Referred Specimens.—V11134.2, a fragmentary maxilla with P$^{3-4}$ from a separate nodule (Fig. 5a, c).

Etymology.—Latin *minor,* indicating the small size of the new species with respect to the type species, *Sarcodon pygmaeus.*

Diagnosis.—Smallest species of *Sarcodon,* M^1 about 70% of the size of *Sarcodon pygmaeus,* and much smaller than *Sarcodon udovichenkoi* (Averi-
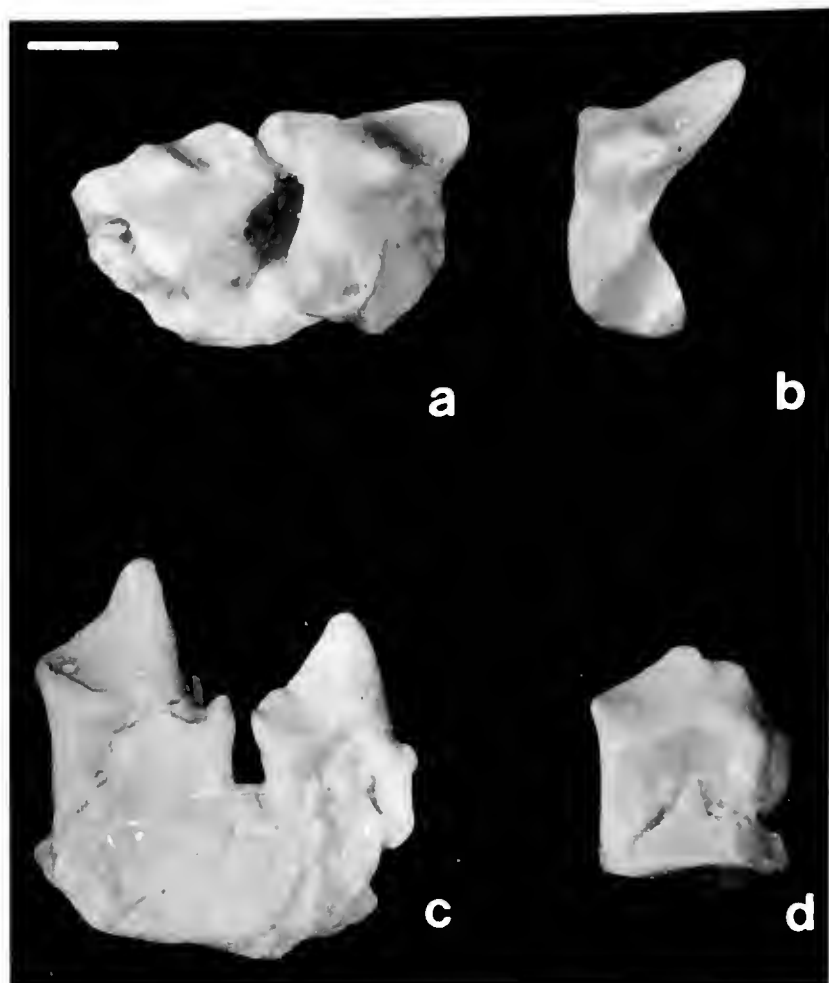
Fig. 5.—*Scardodon minor,* n. sp. Left P$^{3-4}$ (V11134.2) and M^1 (V11134.1, holotype) in occlusal (a, b) and buccal (c, d) views. Scale = 1 mm.

anov, 1994). Metastylar wing and hypoconal shelf less developed than in other species. Similar to *S. pygmaeus* in having closely appressed metacone and paracone, distinguishing these taxa from *S. udovichenkoi.*

Description.—The paracone and metacone on M^1 are slightly divided at their apices; otherwise, they are largely fused (Fig. 5b, d). The metacone, higher than the paracone, sends a strong metastylar wing posterolaterally. The labial surface of this wing is gently concave whereas lingually it bears a narrow shearing facet. The metastyle root is more labially positioned than that of the paracone. The protocone is distinct but is much lower than the metacone and paracone. The weak conules are barely discernible at the bases of the labial cusps. The trigon basin is shallow and oval in outline. The hypocone lies posterolingual to the protocone; although its tip is broken, the hypocone was clearly smaller than in other species of the same genus. Pre- and postcingula are absent.

V11134.2 is believed to be from the same species as V11134.1 because of similar size and morphological compatibility (Fig. 5a, c). P^3 is triangular in crown view and has a main labial cusp, which descends as a crest posteriorly. A weak lingual cusp suggests development of the protocone. P^4 is transversely more elongate than P^3 and bears a more fully developed protocone. The hypocone and hypoconal shelf are much less prominent than those of M^1. A distinct metastylar wing extends posterolabially from the single, strong labial cusp. As on M^1, the lingual edge of the metastylar wing bears a shearing facet, but in contrast to

M^1, P^4 has a weak, conule-less parastyle anterior to the base of the labial cusp.

Measurements (in mm; length, width): V11134.1—M^1 1.95 (lab)–1.24 (lin), 2.72 (ant)–3.15 (post). V1113.2—P^3 1.94, 1.75; P^4 2.26, 2.38.

?*Sarcodon pygmaeus* Matthew and Granger, 1925

Specimens.—V11135 includes a P^4, slightly broken M^1, an isolated ?incisor and premolar, portions of both mandibular rami bearing root fragments and at least one fairly complete premolar, from a single nodule. Further preparation may reveal additional complete cheek teeth, but this procedure is impeded by the disorderly, tightly packed array of bone fragments which make up this nodule. Due to this preservational circumstance, measurements of teeth are currently impractical but they appear to match the type species (AMNH 20427) rather than *Sarcodon minor* in size. We tentatively assign this specimen to *Sarcodon pygmaeus*.

Description.—The mandibular ramus bears two mental foramina, the larger and posterior of which is beneath the anterior root of the tooth here presumed to be P_4. The anterior foramen is presumably in the same position as in specimens from Mongolia (Szalay and McKenna, 1971), under the diastema between the teeth traditionally termed P_2 and P_3, although the alveoli in V11135 cannot be clearly discerned. A broken cross section of the anterior ramus exposing the canine root shows this tooth to have been greatly enlarged. From breakage it can also be seen that the canine root extends at least as far posteriorly as the midpoint between the two mental foramina. On the isolated right $P?_3$, the protoconid apex overlies the anterior of the two roots. A crest curves posteriorly, forming a distinct shoulder. The right P_4 is double-rooted; although somewhat abraded, it is dominated by a large, blunt, conical protoconid flanked by a small posterior cusp.

The upper cheek teeth are far more distinctive. P^4 is unworn and well preserved (the tooth identified by Szalay and McKenna [1971:fig. 11] as P^4 is probably M^1, see below). It is difficult to determine from the damaged roots present in the maxilla anterior to this tooth in AMNH 21732 whether one is counting premolars or a canine. A large cusp, almost certainly the paracone, forms the anterolabial corner of the tooth, towering over all else. There is no trace of a parastyle or metacone. A strong crest extends to the metastylar region, producing a pronounced, vertically inclined, posterolabially facing shearing surface. On the tooth's lingual margin, a distinct protocone is dwarfed by the paracone. A minute hypocone sits on a swollen shelf posterior to the protocone. Cingula are absent.

M^1 is a highly distinctive tooth, showing unmistakable resemblance to AMNH 20427, left upper molar of the holotype of *Sarcodon pygmaeus*. As on the type, in V11135 breakage obscures morphology of the buccal cusp or cusps. An irregularly shaped block of the crown posterior to the anterior base of the paracone and extending into the metastylar region is missing. Nevertheless, from the preserved part of the tooth, as well as from the shape and extent of the block of lost enamel, it is evident that this molar was nearly if not fully zalambdodont. The parastyle is tiny compared to the expanded metastyle. A well-

defined cingulum runs across the external base of the tooth. The tooth's most characteristic area lies posterolingual to the modest protocone; here, from the base of the protocone, a distinctive hypoconal shelf juts posteriorly almost like a peninsula. This shelf is not quite as prominent or extensive as that seen in AMNH 20427, leading us to speculate that this latter specimen might represent M^2 rather than M^1, as it had been identified (with a query) by Szalay and McKenna (1971). In either case, AMNH 20427 and the two upper cheek teeth just described are highly distinctive—there can be little question to refer them to the same or very closely related species.

Comments.—Identification of this taxon's seven postcanine tooth positions has proven controversial. McKenna et al. (1971) and Szalay and McKenna (1971) argued that this taxon possessed only two lower molars (rather than the three traditionally assumed), based on a proposed relationship, now disfavored, between *Sarcodon* and *Deltatheridium*, and the assumption (to our knowledge, still untested) that the last molar (rather than a premolar) "is the tooth most likely to have been lost in animals with prominent shearing modifications of P_4^4–M_2^2" (Szalay and McKenna, 1971:286). In describing *Prosarcodon*, a related Paleocene form from Shanxi Province, McKenna et al. (1984) accepted, without comment, a P_{1-4}^{1-4} M_{1-2}^{1-2} dental formula, despite the strikingly molariform appearance of the teeth in the third to last positions (particularly the lower one). We know of no objective way of deciding whether the "missing" postcanine of *Sarcodon* is a premolar (most likely the first) or a molar (most likely the last); we opt for the traditional interpretation (three premolars and three molars) for the simple reason that it has yet to be conclusively falsified.

We propose using the name "Insectivora" as the stem-based counterpart (de Queiroz and Gauthier, 1990) of Lipotyphla, the latter name being used to designate the clade stemming from the most recent common ancestor of Chrysochloromorpha, Erinaceomorpha, and Soricomorpha (the last three mentioned terms being used sensu MacPhee and Novacek, 1993). McKenna et al. (1984) included *Prosarcodon* within Palaeoryctoidea, which in turn was subsumed within Soricomorpha, arguing that a piriform fenestra in *Prosarcodon* (along with *Sarcodon* and *Sinosinopa*) is indicative of lipotyphlan affinity. These authors advanced no features, however, substantiating specifically soricomorph affinities of these taxa. Butler (1988) and MacPhee and Novacek (1993) questioned the basis of these associations. Thus we are left with little or no evidence to support the hypothesis that any of these forms are members of the clade here designated by the name "Lipotyphla," and even less suggesting the hypoth-
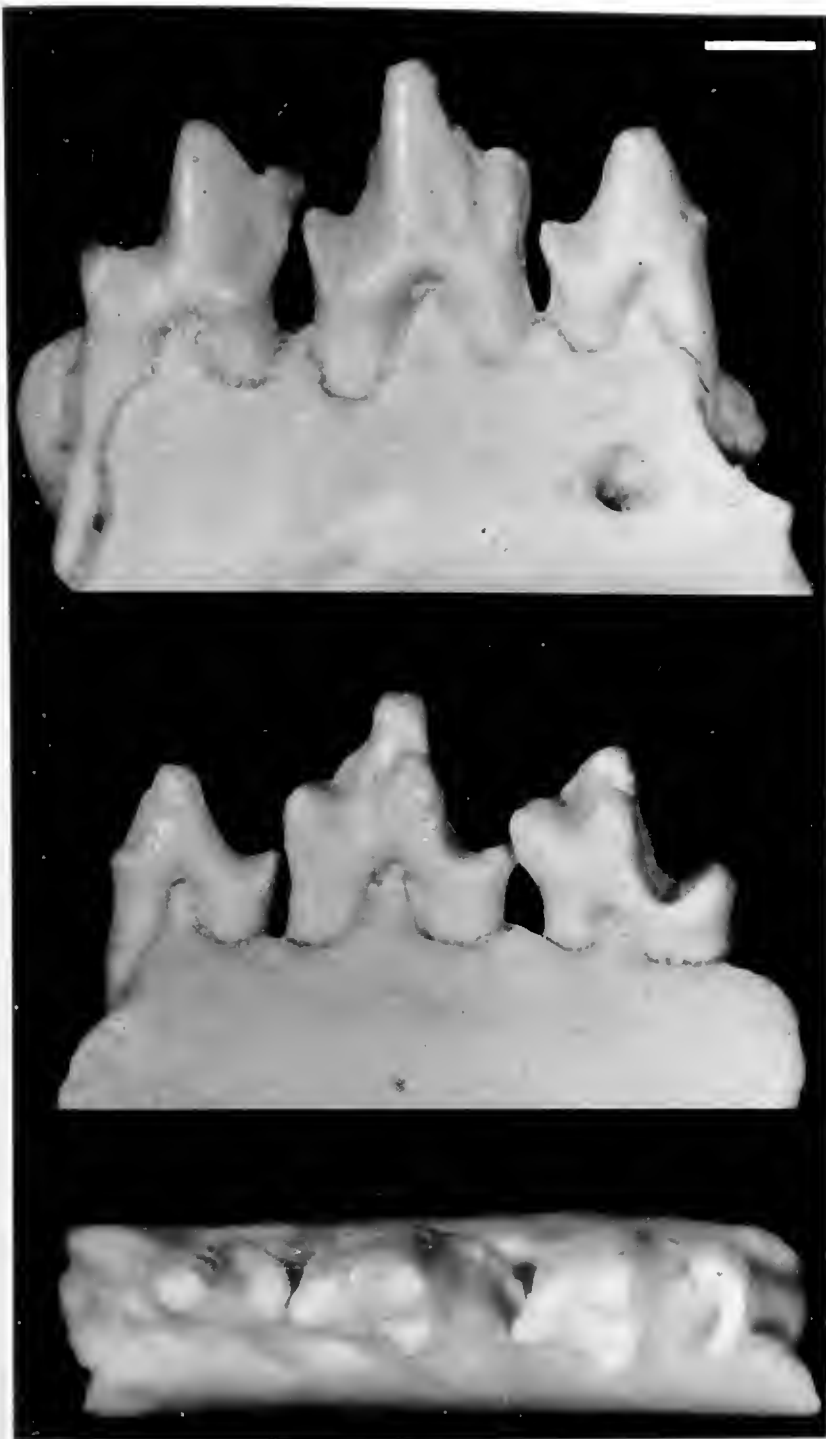
Fig. 6.—*Hyracolestes* sp., cf. *H. ermineus*, right mandible bearing P_3–M_1 (V11136) in buccal (top), lingual (middle), and occlusal (bottom) views. Scale = 1 mm.

esis that they are soricomorphs; at this juncture we see no better alternative than to regard them as Insectivora incertae sedis.

Hyracolestes sp., cf. *H. ermineus* Matthew and Granger, 1925
(Fig. 6)

Specimen.—A fragmentary right mandible with P_3–M_1 (V11136).

Description.—The specimen was surface collected and consequently the tooth enamel is slightly eroded. As in the type (AMNH 20425), there is a single, large mental foramen under P_3 on the labial side of the ramus (Fig. 6). The crown pattern of P_3–M_1 compares closely to the type specimen (Matthew and Granger, 1925; Szalay and McKenna, 1971). The trigonid of P_4 is longer, narrower, and more open than that of M_1. The labial

surface of the protoconid and paraconid forms a gently curving prevallid that bears a carnassial edge on P_4 and M_1. Although the enamel is worn, a distinct notch is visible between the protoconid and paraconid on P_4 and M_1.

Measurements of V11136 (in mm; length, width): P_3 1.53, 0.75; P_4 2.04, 1.20; M_1 2.01, 1.30.

Comments.—V11136 differs from the holotype (AMNH 20425) in being smaller and slightly lower crowned. The M_1 hypoconid in the holotype is broken; the posterior cusp on the talonid is assumed to be a hypoconulid, whereas the entoconid is absent, leaving the talonid open lingually (Szalay and McKenna, 1971). On the new specimen, however, the posterior talonid cusp is situated further lingually, making it more likely to be an entoconid than a hypoconulid, but the talonid remains open lingually. In terms of size, crown height, and position of the talonid cusp, the Bayan Ulan specimen is more similar to *Hyracolestes ermineus* from Qianshan (Qiu and Li, 1977). The Qianshan fauna has recently been assigned to the early late Paleocene Nongshanian Chinese mammal age (Tong et al., 1995). Russell and Dashzeveg (1986) assigned with uncertainty one lower molar from the Bumban Member to *Hyracolestes*. This tooth differs from other specimens of *Hyracolestes* in being larger and in having a distinct hypoconulid and entoconid. If proven to belong to *Hyracolestes*, this tooth most likely represents M_2, as this is the only molar in *Hyracolestes* to bear a distinctive hypoconulid and entoconid.

The phylogenetic position of *Hyracolestes ermineus* remains puzzling. Matthew and Granger (1925) considered it to be a carnivoran of shrew-like size, placing it tentatively in the Creodonta. Van Valen (1966) referred *Hyracolestes*, along with *Praolestes* and *Sarcodon* (= *Opisthopsalis* [Szalay and McKenna, 1971]), to the Erinaceoidea, a relationship rejected by Szalay and McKenna (1971). Instead, recognizing its similarities to *Sarcodon* and *Deltatheridium*, Szalay and McKenna (1971) considered *Hyracolestes*, *Sarcodon*, and *Deltatheridium* to be deltatheridiid palaeoryctoid insectivorans. Qiu and Li (1977), however, placed *Hyracolestes* within the Deltatheridia as family indet. In their description of *Prosarcodon*, McKenna et al. (1984) removed *Sarcodon* from Deltatheridiidae, grouping it with *Prosarcodon* and *Sinosinopa* (Qi, 1987) in Micropternodontidae under Soricomorpha; *Hyracolestes* was left in isolation, recently being treated as family and order indet. (Russell and Zhai, 1987). Our new specimen provides little additional morphology helpful for resolving the phylogenetic position of

Fig. 7.—Palacoryctoidea, incertae sedis, right M^{2-3} and P^4 (V11137) in occlusal (top), buccal (middle), and anterior (bottom) views. Scale = 1 mm.

The paracone is the highest cusp, immediately followed by a lower metacone. Between the protocone and the labial cusps is a trough oriented longitudinally. There are no conules or cingula. Assuming a usual eutherian dental formula, the two molars are referred to as M^2 and M^3, although they may actually be M^1 and M^2 (Fig. 7). The two teeth are broken at their lingual apices, preventing accurate measurements of tooth width. Nonetheless, it is certain that these teeth are transversely elongate and anteroposteriorly short. On M^2 the paracone is larger and more lingually placed than the metacone. The prominent parastyle projects anterolabially. A crest is formed along the posterior side of the metacone to the metastyle; the latter is less developed than the parastyle. Between the parastyle and metastyle the ectoflexus is deep. The protocone is broken. From what is preserved, it appears that the hypocone and cingula are absent. The conules, if present, are completely worn. M^3 is much smaller in all dimensions than M^2. The metacone is greatly reduced and the metastyle is absent.

Measurements of V11137 (in mm; length, width; * = estimated): P^4 2.38, 2.07; M^2 2.05, 2.90*; M^3 1.48, 2.4*.

Comments.—The transversely elongate molars, anterolabially extended parastyle on M^2, and likely absence of a hypocone are suggestive of palaeoryctoid rather than leptictoid features. In general, these teeth resemble *Cimolestes* with the exception that M^3 is proportionally more reduced than in *Cimolestes*. V11137 compares also in general shape with *Naranius* Russell and Dashzeveg, 1986, from the Bumban fauna of Mongolia. However, *Naranius* (Russell and Dashzeveg, 1986:fig. 7a) differs from the Bayan Ulan specimens in being anteroposteriorly shorter, considerably smaller, in its more prominent metastyle, deeper M^2 ectoflexus, broader labial cingulum, and better developed posterior cingulum.

?Leptictidae
New genus and species

Specimen.—A left mandible with complete dentition from a peanut-sized pellet. Associated with it are a partial right mandible with I_3–M_3, and a fragmentary maxilla with some teeth. In addition to these dental remains, postcranial skeletal elements are also preserved in the same nodule. Of particular interest among these are articulated structures of the pes. These specimens are extremely small and delicate, making preparation painfully slow. Therefore, we defer more detailed analyses of this material to subsequent studies, noting here only that in possessing a submolariform P_4 and transversely elongate molars, with the protocone aligning with the paracone, and development of a hypocone, this taxon seems to have leptictid affinities.

this taxon but serves as another biostratigraphic link between the Bayan Ulan, Gashato, and Qianshan faunas. Given the similarities with *Sarcodon* pointed out by Szalay and McKenna (1971), and our discussion above concerning the taxonomic placement of *Sarcodon*, we regard *Hyracolestes* as well as Insectivora incertae sedis.

Palaeoryctoidea Winge, 1917, incertae sedis
(Fig. 7)

Specimens.—V11137, right P^4 and ?M^{2-3} from one coprolitic nodule.

Description.—The tricuspate P^4 is well preserved (Fig. 7). The protocone is distinct but low, aligning with the paracone.

Fig. 8.—*Prolimnocyon chowi*, n. sp. Left mandible preserving M_{2-3} and roots of $P_4–M_1$ (V11138, holotype) in buccal (top), lingual (middle), and occlusal (bottom) views. Scale = 2 mm.

Creodonta Cope, 1875
Hyaenodontidae Leidy, 1869
Limnocyoninae Wortman, 1902
Prolimnocyon Matthew, 1915
Prolimnocyon chowi, **new species**
(Fig. 8, 9)

Holotype.—A left dentary with M_{2-3} and roots of $P_4–M_1$ (V11138; Fig. 8).

Referred Specimens.—A right M^1 (V11139.1) and the labial half of a left M^1 (V11139.2) (Fig. 9).

Etymology.—Named in memory of Dr. Minchen Chow (November 9, 1918–January 4, 1996), the founding father of Chinese paleomammalogy and our teacher and friend.

Diagnosis.—Smaller than other species of *Prolimnocyon* except *P. eerius*. Differs from other species of the genus in having a short metastylar blade, labial outline of M^1 straight, minute cuspules on the labial cingulum, posterior contour of M^1 curved, distinct conules closer to the protocone than to labial cusps, slender protocone, little shear contrib-

uted by the metacone, no shear from protocone, trigonid of M_2 anteroposteriorly compressed and wider than that of M_1, and M_3 significantly reduced but, relative to M_2, less so than in other species of the genus.

Description.—A small creodont, similar to *Prolimnocyon eerius* Gingerich (1989) in size, is represented in the Bayan Ulan fauna. On the holotype, the P_4 and M_1 are broken, but their roots permit reasonable estimation of size (Fig. 8). The M_1 is identified on the basis that it is the longest tooth and its anterior root is wider than the posterior one, suggesting a sizable trigonid. In addition, the distinctive hypoflexid also indicates a well-developed talonid posteriorly and a large trigonid anteriorly, similar to the form of M_2. Apart from the broken apex of the protoconid, the crown of M_2 is well preserved, little worn, and wider than M_1. The paraconid is markedly larger and taller than the metaconid. The paraconid and metaconid are relatively closely spaced, two lines joining these cusps to the protoconid forming an acute angle. Judging from the cross section of its base, the protoconid was by far the largest trigonid cusp. There is a faint cingulid on the anterior base of the trigonid, which terminates lingually at a contact facet caused by M_1. The trigonid is of moderate height and the talonid is considerably narrower and
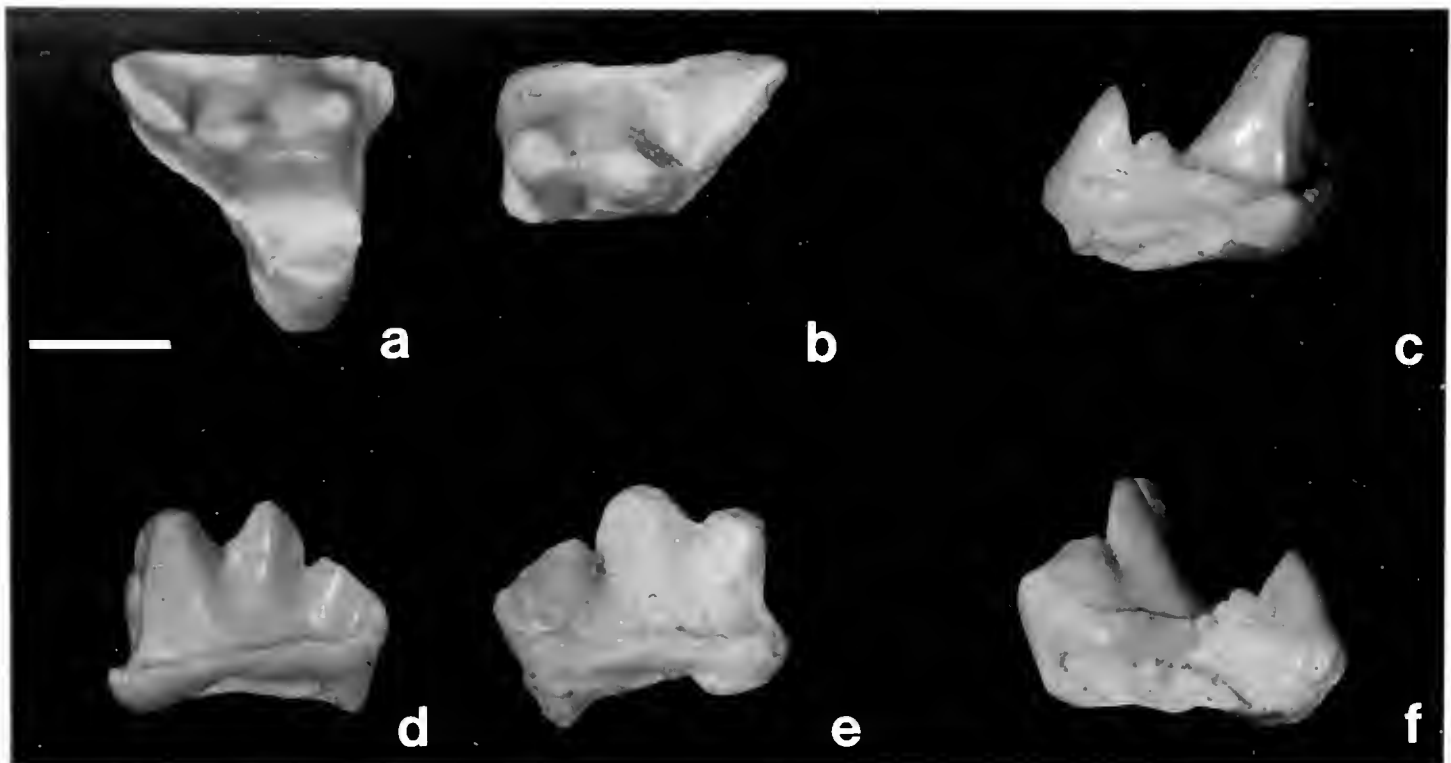
Fig. 9.—*Prolimnocyon chowi*, n. sp. a, b. Occlusal views of right M¹ (V11139.1, a) and buccal half of left M¹ (V11139.2, b). d, e. Buccal views of the same teeth. c, f. Anterior (c) and posterior (f) views of V11139.1. Scale = 2 mm.

shorter than the trigonid. The cristid obliqua joins the vertical wall of the trigonid relatively medially, lending the narrow talonid a "waisted" appearance anteriorly. The hypoconid is the largest talonid cusp, flanked posteromedially by a much smaller hypoconulid, the two cusps being separated by a narrow gap. A valley parallel to the cristid obliqua is defined by the hypoconid and hypoconulid. A distinct entoconid, the smallest talonid cusp, occurs on the posterolingual part of the talonid; anteriorly the talonid opens lingually.

The double-rooted M_3 is well preserved (Fig. 8). It is considerably smaller than M_2, but is proportionally less so than in other species of the genus (e.g., Gingerich, 1989; Gingerich and Deutsch, 1989; Gebo and Rose, 1993). The trigonid is open lingually and is, in relation to the talonid, lower and narrower than that of M_2. The protoconid and paraconid are subequal in size, while the metaconid is the smallest trigonid cusp. The protoconid is separated from the paraconid and metaconid by notches, and the trigonid is open lingually. There is a cusp-like projection at the anterior base of the protoconid, suggesting the presence of a rudimentary anterior cingulid. The cristid obliqua is more labially placed than that on M_2, joining anteriorly the ridged posterior wall of the protoconid. The hypoconulid is the largest talonid cusp and has a rounded posterior outline.

On the right M¹ (V11139.1) the paracone, although slightly worn at the tip, is the highest cusp of the tooth and is slightly more labial than the metacone (Fig. 9). The parastyle is small. The metacone is slightly less elevated and smaller than the paracone. From the bottom of the trigon basin, these two cusps are joined along about two-thirds of their height; their tips are well separated. In contrast to the parastyle, the metastyle is well developed, forming a moderate metastylar blade which extends posterolabially. Wear on the metastyle indicates development of metacrista shear. The metastyle and metacone are separated by a distinct carnassial notch. Only slight wear is visible on the anterolingual side of the metacone. A low external cingulum runs the full length between the parastyle and metastyle. The cingulum bears numerous minute cusps in V11139.1, whereas on the left M¹ (V11139.2) of an older individual, these cusps are nearly completely worn (Fig. 9). The labial outline of the tooth is

straight, while the anterior contour is curved. The low protocone is flat labially and rounded lingually, aligning with the paracone. The paraconule and metaconule are small and subequal in size; both are separated from the protocone by narrow notches. The weak postmetaconule crista runs onto the metastylar blade along the posterior base of the tooth and is punctuated by narrow gaps, while the similarly weak preparaconule crista extends to the parastyle. Faint cingula occur along the anterior and posterior bases of the protocone. V11139.2 has a slightly longer metastylar blade and larger shearing facet on the blade than does V11139.1, possibly reflecting greater wear. The referral of upper molars to this taxon is based on the matching size and morphology with the lower teeth, including details such as the moderate metastyle in relation to the anteroposteriorly compressed trigonid.

Measurements (in mm; length, width; * = estimated): V11138 (holotype)—P_4 >3.5, —, M_1 4.45*, —; M_2 4.38. 3.16 (tri)–1.87 (tal); M_3 2.74, 1.63 (tri)–1.14 (tal). V11139.1—M¹ 4.11, 4.05. V11139.2—M¹ 4.24, —.

Comments.—The presence of three molars in the lower jaw excludes V11138 from being a viverravid carnivore. The distinctive metastylar blade on M¹ and carnassial M_2 (and probably M_1 as well) secure the placement of the Bayan Ulan material in the Creodonta. The great reduction of M_3 is diagnostic of *Prolimnocyon*, the only creodont genus possessing this feature (Gingerich, 1989; Gingerich and Deutsch, 1989). About five species of the genus have been described, all from North America: *P. atavus* Matthew, 1915; *P. antiquus* Matthew, 1915; *P. elizabethae* Gazin, 1952; *P. haematus* Gingerich and Deutsch, 1989; and *P. eerius* Gingerich, 1989. Among these forms, *P. elizabethae* is only questionably distinct from *P. atavus* and *P. antiquus* (Gingerich and Deutsch, 1989). Aside from the questionable identification of fragmentary teeth

from the middle Paleocene of southern Wyoming (Rigby, 1980) as "*Prolimnocyon*," *P. eerius* from the earliest Wasatchian of the Clarks Fork Basin, Wyoming, is the earliest known species of *Prolimnocyon* in North America (Gingerich, 1989). Being the smallest member of the genus, *P. eerius* compares closely with *P. chowi* in size. However, *P. eerius* is more derived than *P. chowi* in having a more extended metastylar blade and closely appressed metacone and paracone on M^1. No lower teeth of *P. eerius* are currently known. In addition to molar morphology, *P. chowi* differs from other species of the genus in being distinctively smaller, having a shorter metastylar blade, and a relatively less reduced M_3.

Among other creodonts, the M^1 (V11139.1) of *P. chowi* is also comparable to an M^1 referred to as cf. *Acarictis ryani* from the Four Mile fauna of Colorado (Polly, 1993; UCMP 44302; cast AMNH 129782) in having small size, a moderate metastylar blade, straight labial outline, and minute cuspules on the labial cingulum. *Acarictis ryani* is named on the basis of only lower dentition, except a P^3, from the middle and late Sandcouleean subage of the Wasatchian Land Mammal Age, Clarks Fork Basin, Wyoming (Gingerich and Deutsch, 1989). The types of *Acarictis ryani* and *P. eerius* are from the same area and are similar in size; whether they are in fact distinct would seem to warrant further consideration. A sizable M_3 is assumed for *Acarictis ryani* from a wear facet on the posterior wall of M_2 in the type (UM 79081) and from the anterior alveolus of referred specimens (Gingerich and Deutsch, 1989); a conclusive resolution of the status of *Acarictis ryani* requires discovery of its M_3.

The Four Mile M^1 of cf. *Acarictis ryani* (Polly, 1993) displays several differences from the Bayan Ulan specimen, including less developed conules, stronger postmetaconule crista but weaker preparaconule crista, a protocone slightly more robust at its base, parastyle more reduced, and less curved posterior contour. The metastylar blade of the Four Mile specimen appears shorter, but this probably results from erosion of the posterior end of the metastyle.

Other hyaenodontids, including small species such as *Prototomus deimos* (Gingerich and Deutsch, 1989; Polly, 1993), are clearly distinguishable from the Bayan Ulan taxon in their more extended metastylar blades, which result in the posterior and labial edges of the tooth forming a more acute angle. With posterolabial lengthening of the metastyle, the labial edge of the tooth becomes more curved,

whereas the posterior side is straighter and longer in crown view. In conjunction with metastylar enlargement in more advanced forms, the posterolingual side of the metacone and the posterior side of the protocone develop shearing facets.

More precise phylogenetic placement of the Bayan Ulan taxon within *Prolimnocyon* requires more complete material. Nonetheless, the new taxon appears to be the oldest and most primitive species of the genus and among the earliest creodonts known from Asia. *Oxyaena* sp. and *Sinopa* sp. have been reported by Dashzeveg (1982a, 1988) from the Naran Member of the Naran Bulak Formation in the Nemegt Basin, Mongolia, but this material was unavailable to us for comparison.

<div align="center">

?Creodonta
Family indeterminate
(Fig. 10)

</div>

Material.—V11140.1, a right M_1, from one coprolitic nodule and V11140.2, a left M_1 from a separate nodule (Fig. 10).

Description.—The M_1 has a high trigonid which opens lingually. The paraconid is by far the smallest and lowest trigonid cusp, extending anterolingually. The sharply pointed protoconid forms the highest cusp, and is separated from the paraconid and metaconid by narrow notches. Its lingual surface is vertical, contrasting with a more gently sloping labial surface; its anterior edge is sharp and straight. There is no shearing facet on the labial surfaces of the paraconid and protoconid. The metaconid bears a labially directed protocristid. The paraconid and protoconid outline a low anterior valley; the protoconid and metaconid define a posterior valley which is more elevated than the anterior one. The two valleys incline medially and merge at the lingual base of the trigonid. The posterior face of the trigonid does not form a smooth and vertical wall; rather, the posterior surface of the protoconid is offset anteriorly with respect to the posterior surface of the metaconid. The talonid is low and much shorter than the trigonid. The hypoconid is the largest talonid cusp, with an anterolingually extending cristid obliqua. The hypoflexid is broad and deep. The hypoconulid is the smallest of the talonid cusps; it is buccally positioned, being closer to the hypoconid than to the entoconid. The entoconid, the lowest talonid cusp, forms a low ridge. The talonid basin is open lingually.

Measurements (in mm; length, width): V11140.1—M_1 4.48, 1.93 (tri)/1.82 (tal). V11140.2—M_1 4.18, 1.84 (tri)/1.53 (tal).

Comparisons.—At first glance the M_1 looks deceptively similar to that in early carnivorans. There are critical differences, however, between this Bayan Ulan taxon and miacids and viverravids. The protoconid in the Bayan Ulan specimens is pointed and unflared, in contrast to carnivorans. The paraconid is considerably lower than the protoconid and the cutting edge of the paracristid is poorly developed. The trigonid opens more widely than in carnivorans. Most importantly, there are no shearing
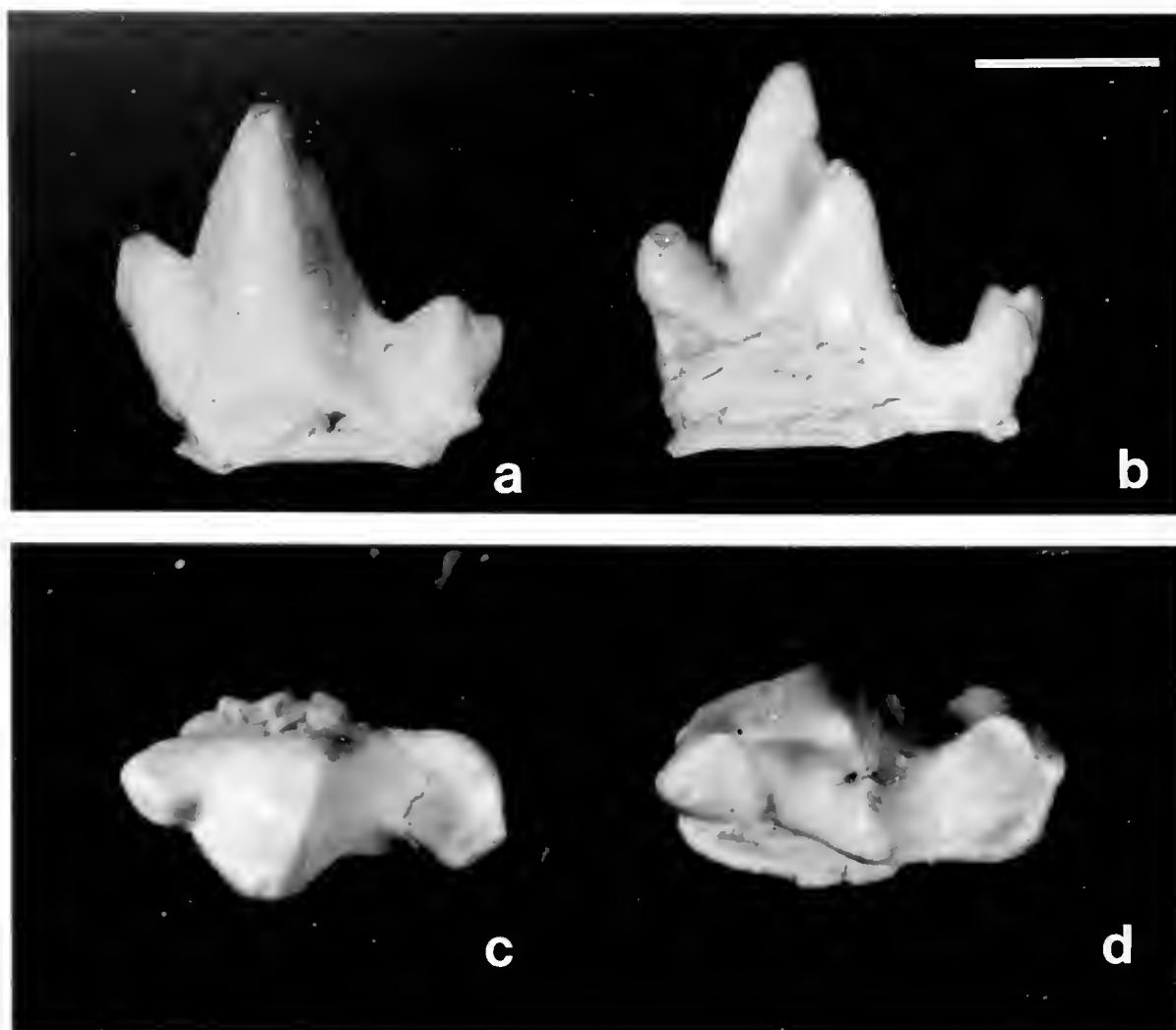
Fig. 10.—?Creodonta, family indet. a, c. Left M_1 (V11140.2) in buccal (a) and occlusal (c) views. b, d. Right M_1 (V11140.1) in lingual (b) and occlusal (d) views. Scale = 2 mm.

facets on the labial surfaces of the paraconid and protoconid indicating presence of specialized post-vallum–prevallid shear against P^4, nor do such facets occur on the posterior surface of the trigonid. Finally, there is no carnassial notch between the protoconid and the paraconid.

These two Bayan Ulan molars also resemble M_1 of early creodonts. In size and talonid shape, for example, they match the lower molars of *P. chowi*. However, the trigonids of these two molars seem too narrow and too open lingually, relative to M_2 in *P. chowi*, to suggest an association. The paraconid extends further anteriorly than in any known creodont, and, again, lack of shearing facets on the protoconid and paraconid argues against creodont affinities. Eventually, these teeth may be shown to represent either a new taxon or to be dP_4s of *Prolimnocyon chowi*. At present, we tentatively regard these teeth as pertaining to creodonts.

Carnivoramorpha Wyss and Flynn, 1993
Viverravidae Wortman and Matthew, 1899
cf. *Viverravus* sp.
(Fig. 11)

Specimen.—V11141, a fragmentary left lower jaw containing the posterior half of P_3 and a complete P_4 (Fig. 11).

Description.—The P_3 consists of a sharp main cusp followed by a minute accessory cuspule posteriorly (Fig. 9). The well-preserved P_4 is blade-like, consisting of four longitudinally aligned cusps. The main cusp is flanked by a small cusp anteriorly and two posteriorly, which together constitute an elongate talonid. The more anterior of the two posterior cusps is slightly more labially positioned. Notches occur between the main cusp and the first posterior cusp, and between the two posterior cusps. The alveolus preserved posterior to P_4 is broad, suggesting a sizable M_1, a condition typical in carnivorans.

Measurements of V11141 (in mm; length, width): P_4 2.88, 1.07.

Comments.—Although highly variable, an elongate talonid bearing two posterior cusps on P_4 as shown in V11141 has been considered a diagnostic feature of "Carnivora" and is absent in plausible carnivoran outgroups such as creodonts (Flynn and Galiano, 1982). Wyss and Flynn (1993), however, did not use this feature to diagnose their taxon Carnivoramorpha, a term roughly equivalent to "Carnivora" of Flynn and Galiano (1982). Nonetheless, the best taxonomic assignment we can make based on available material is that V11141 represents a viverravid.

Paleocene and early Eocene carnivorans reported from South China (Zheng et al., 1975; Qiu and Li, 1977; Wang, 1978) are generally larger than the Bayan Ulan specimen. The Bayan Ulan specimen is
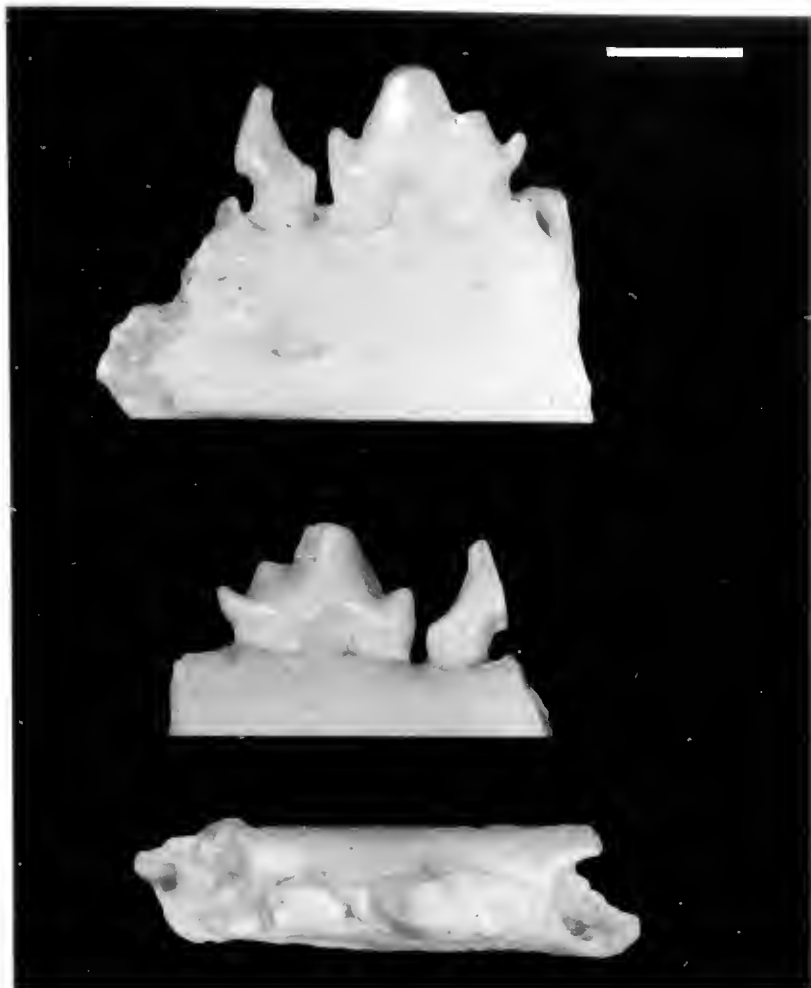
Fig. 11.—Cf. *Viverravus* sp. Left mandible preserving posterior part of P$_3$ and complete P$_4$ (V11141) in buccal (top), lingual (middle), and occlusal (bottom) views. Scale = 2 mm.

Fig. 12.—*Pseudictops lophiodon*, left mandible preserving P$_4$–M$_3$ and roots of C$_1$–P$_3$ (V11142.1) in occlusal (top), buccal (middle), and lingual (bottom) views. Scale = 10 mm.

more closely comparable with such North American taxa as *Simpsonictis* and *Protictis* in size and morphology. A P$_4$ of a possible viverravid from Morocco (Gheerbrant, 1995) is much smaller than V11141; the talonid of the former is basined, an unusual feature for early carnivorans. Other than documenting the first occurrence of a viverravid carnivoran in the Paleocene of the Mongolian Plateau, the limited material currently available precludes more definitive interpretation.

Anagalida Szalay and McKenna, 1971
Pseudictopidae Sulimski, 1968
Pseudictops lophiodon Matthew, Granger and
Simpson, 1929
(Fig. 12)

Specimens.—V11142.1, a left lower mandible with P$_4$–M$_3$ and roots of C–P$_3$ (Fig. 12); V11142.2 a fragmentary mandible with the talonid of M$_2$; V11142.3, a fragmentary mandible with dP$_4$, erupting P$_4$, and M$_1$; V11142.4, a maxilla with damaged P^3–M^3; V11142.5, a maxilla with broken teeth; V11142.6, a fragmentary mandible with broken dP$_4$–M$_2$ and erupting P$_3$ and M$_3$.

Description.—The lower dental formula is ?–1–4–3. The ca-

nine is robust. The P$_1$ and P$_2$ are single- and double-rooted, respectively. As shown in V11142.3, dP$_4$ is molariform, possessing a lingually open trigonid that consists of distinct protoconid, paraconid, and a larger metaconid. The basined talonid of dP$_4$ bears the hypoconid, entoconid, and hypoconulid, of which the hypoconid is the largest and the hypoconulid forms an anteroposteriorly compressed ridge. The trigonid of dP$_4$ is low and as wide as the talonid. The P$_4$ differs from dP$_4$ in being larger and having a reduced paraconid and a simple talonid that bears a single, labially placed cusp. The trigonid is anteroposteriorly compressed but is much higher than the talonid. The M$_1$ differs from P$_4$ mainly in having a well-developed talonid similar to that of dP$_4$. The talonid cusps are indistinguishable on worn molars, forming a ridge that encircles a basined talonid. Because it possesses a hypoconulid lobe, M$_3$ is the longest molar; its talonid is narrower than the trigonid. The hypoconulid is the most elevated talonid cusp and sits nearer the hypoconid than the entoconid. The entoconid blocks the talonid basin lingually.

Comments.—*Pseudictops* has been thoroughly reviewed by Sulimski (1968), who erected for it the monotypic family Pseudictopidae. This genus has been recorded at several localities on the Mongolian Plateau, including Nomogen (Chow and Qi, 1978), Gashato, and Naran Bulak (Matthew et al., 1929; Sulimski, 1968). A second species, *P. chaii*, based on a partial lower jaw bearing M$_3$, was reported from the late Paleocene Taizicun Formation by

Tong (1978). *Pseudictops* is perhaps the best "index" taxon for local biostratigraphic correlation because of its restricted distribution within the supposed late Paleocene fauna (Nomogen, Gashato, Naran, and Bayan Ulan); it has not been reported from early Eocene beds of Mongolia, such as the Bumban Member of the Naran Bulak Formation (Dashzeveg, 1988).

Glires Linnaeus, 1758
Eomylus borealis (Chow and Qi, 1978)

Mimotona borealis Chow and Qi, 1978:79.
Eomylus borealis Dashzeveg and Russell, 1988:138.

Comments.—The holotype of *Eomylus borealis*, a right lower jaw with P_4–M_2 (V5531) from the Nomogen fauna, was only briefly described in its original publication (Chow and Qi, 1978), in which the species was named "*Mimotona*" *borealis*. Noting its single pair of lower incisors, a typical "eurymylid" feature, Dashzeveg and Russell (1988) transferred the species to their new genus *Eomylus*, making the new combination *Eomylus borealis*. The type species of the new genus, *Eomylus zhigdenensis*, is established on material recovered from the Zhigden Member of the Naran Bulak Formation at the Tsagan–Khushu locality, Nemegt Basin, southern Mongolia. Dashzeveg and Russell (1988) also reallocated five fragmentary jaws and an isolated M_1 from the Bayan Ulan fauna, which had been referred to "*Mimotona*" *borealis* in previous listings (Russell and Zhai, 1987), to the genus *Eomylus* as well. Based on additional material recently recovered from Bayan Ulan, we recognize at least two taxa of gliriform eutherians, not including *Tribosphenomys*, in the fauna (see below). Because preparation of these specimens is not yet completed, the gliriform mammals from Bayan Ulan will be considered more fully in a separate study. Only a few preliminary observations are offered here.

Referral of the Bayan Ulan and Nomogen specimens to *Eomylus* requires further consideration, inasmuch as the diagnosis for *Eomylus* (Dashzeveg and Russell, 1988) is based exclusively on the upper dentition, whereas the Bayan Ulan and Nomogen specimens available to Dashzeveg and Russell consisted solely of lower teeth. The characters that distinguish *E. borealis* from *E. zhigdenensis*, according to Dashzeveg and Russell, are its greater size and presence of a deep groove on the lower molars between the hypoconid and hypoconulid. In addition, we think the wear patterns of the lower teeth of these two taxa are quite different. Upper teeth of *Eomylus* are now known from Bayan Ulan, and it

is possible that *E. borealis* may belong to a different genus. We also observed several differences between the lower teeth of the Nomogen specimen and those from Bayan Ulan. For instance, one perfectly preserved P_4 contained in a mandible from Bayan Ulan referred to *E. borealis* by Dashzeveg and Russell is not only distinct from that of the type species *E. zhigdenensis* (PSS 20-133, Dashzeveg and Russell, 1988:fig. 7) but also from the holotype of *E. borealis* (V5531; Dashzeveg and Russell, 1988:fig. 8). This indicates that specimens from Nomogen and Bayan Ulan may be referable to different species.

?*Khaychina elongata* Dashzeveg and Russell, 1988

Comments.—Specimens provisionally referred to this taxon remain incompletely prepared. These specimens differ from those allocated to *E. borealis* in several features, most importantly the condition of the lower incisor. In specimens assigned to *E. borealis*, the lower incisor lies within the mandible lateral to the roots of the cheek teeth and extends at least to the level of M_2. By contrast the incisor in ?*Khaychina* is positioned ventral to the premolar roots and terminates anterior to the first molar. In *E. borealis*, therefore, the mandibular corpus is swollen whereas in ?*Khaychina* it is much slimmer in cross section. The presence of a long diastema in a fragmentary lower jaw currently exposed is the main reason that we tentatively refer these specimens to ?*Khaychina elongata* (Dashzeveg and Russell, 1988). Further preparation and study may show that recognition of a new taxon is warranted.

Tribosphenomys minutus Meng, Wyss, Dawson, and Zhai, 1994

Comments.—The holotype (V10775), a left maxilla bearing P^3–M^2, associated mandible with P_4–M_3, and sundry isolated incisors and molars have been published (Meng and Wyss, 1994; Meng et al., 1994). Accordingly, this taxon receives little further description here. Nonetheless, it is worthwhile commenting on a new mandible preserving P_4–M_3, collected in 1995. In contrast to the holotype, in which the last premolar is molariform, P_4 in the new specimen is nonmolariform. This suggests either that the new specimen represents a new taxon or that the molariform last premolars in the holotype are deciduous teeth. Previously described specimens are little worn, representing ontogenetically young individuals, whereas the new specimen is certainly older, displaying decreasing degrees of wear on M_1

through M_3. Thus, it seems likely that the last premolar in the holotype is a deciduous tooth, and that replacement of dP_4 in *Tribosphenomys* is delayed.

There are conflicting views concerning the higher-level taxonomy of *Tribosphenomys*, although few question its phylogenetic placement (Meng and Wyss, 1994; Dawson and Beard, 1996). Taxonomic names, such as "Rodentia," are used to designate (via a definition) particular phylogenetic entities or clades (de Queiroz and Gauthier, 1990, 1992). Constructing a taxonomy of gliriform eutherians entails, therefore, deciding which names are to be associated with which clades. We have argued elsewhere that the name "Rodentia" is most appropriately linked to the clade stemming from the most recent common ancestor of Recent eutherians generally termed rodents (i.e., the crown clade). Inasmuch as *Tribosphenomys*, in conjunction with *Alagomys*, represents the nearest outgroup to the crown clade, *Tribosphenomys* is not a member of the clade that we have elected to associate with the name "Rodentia"; taxonomically, therefore, *Tribosphenomys* is not a rodent by definition. This reflects no change in the phylogenetic position of *Tribosphenomys*, but only that the clade stemming from the most recent common ancestor of *Tribosphenomys* and the crown group deserves a different name. We have proposed that this more inclusive clade be designated Rodentiaformes (Wyss and Meng, 1996).

With regard to the phylogenetic placement of *Tribosphenomys*, we wish to clarify our position on the use of incisor enamel structures for reconstruction of rodent phylogeny. Dawson and Beard (1996) state that "Meng and Wyss (1994) are of the opinion that *Tribosphenomys*, which is clearly related to *Alagomys*, is not a rodent, because its incisor enamel, although two-layered, has no HSB. Using this one character does little to explain relationships for animals that are otherwise very rodent-like." Koenigswald (1995:605), responding to our work, stated: "Most recently *Tribosphenomys* was described as an early rodent [Flynn, 1994; Meng et al., 1994] using this set of characters [the number of layers in the incisor enamel]." After an analysis of the distribution of enamel characters in an array of gliriform eutherians, Koenigswald (1995:611) concluded: "Thus the existence of two layers in the incisor enamel in *Tribosphenomys* does not argue necessarily for a close relationship to rodents." As argued above and elsewhere (Meng and Wyss, 1994; Wyss and Meng, 1996), our position of not calling *Tribosphenomys* a rodent has nothing to do with characters, Hunter-Schreger bands included. This matter

strictly concerns the naming of elements within a phylogeny (definition, sensu de Queiroz and Gauthier, 1990, 1992) rather than the process by which those elements are recognized (diagnosis).

The number of incisor enamel layers is one of many characters that we employed in our original analysis to establish the phylogenetic position of *Tribosphenomys*; the optimization of this character did not prove unambiguous, however (Meng et al., 1994:fig. 3). Obviously, evidence of the number of enamel layers alone is inadequate to address the phylogenetic position of *Tribosphenomys*, or any gliriform. Indeed, we previously questioned the phylogenetic utility of this character: "Considering its distribution against other features, we do not think the presence of single-layered incisor enamel in itself to be decisive evidence regarding the inclusion or exclusion of *Alagomys* from Rodentia. By the same token, double-layered enamel is insufficient grounds to consider *Eurymylus* and *Heomys* members of the Rodentia. In short, the number of incisor enamel layers does not provide an infallible demarcator between rodents and their near allies" (Meng and Wyss, 1994:194).

Eutheria incertae sedis
Arctostylopida Cifelli, Schaff, and McKenna, 1989
Arctostylopidae Schlosser, 1923
Palaeostylops iturus Matthew and Granger, 1925

Comments.—The morphology of this taxon is documented in several previous works (Matthew and Granger, 1925; Matthew et al., 1929; Chow and Qi, 1978) and was extensively studied by Cifelli et al. (1989), making additional description unnecessary. *Palaeostylops iturus* is differentiated from *Gashatostylops macrodon* by its smaller size and other dental features (Matthew et al., 1929; Cifelli et al., 1989). As diagnosed by Cifelli et al. (1989: 11), *P. iturus* "differs from *Gashatostylops macrodon*, the most closely similar form, in having a strong sulcus separating the lingual cusps of M^1, three upper incisors, and an unconstricted snout, and in lacking cuspules on upper molar lingual cingula and relative enlargement of the upper and lower second molars." The supposed generic level differences, primarily three pairs of upper incisors, are rarely preserved in specimens from Bayan Ulan (see below).

Palaeostylops iturus is represented by a large number of specimens; after *Lambdopsalis* it is the most common taxon at Bayan Ulan. As in the Gashato and Nomogen faunas, this species numerically dominates its sister taxon *Gashatostylops* (= *Pa-*

laeostylops) *macrodon* (see below). Abundance of *P. iturus* at Bayan Ulan can be partly attributed to the activities of carnivorous predators, as the majority of specimens have been recovered from coprolites. This taphonomic factor probably skews the richness of this taxon relative to others within this fauna.

Gashatostylops macrodon
(Matthew, Granger and Simpson, 1929)

Palaeostylops macrodon Matthew et al., 1929:11.
Gashatostylops macrodon Cifelli et al., 1989:15.

Referred Specimen.—A left rostrum with roots of two incisors on both sides, left C–M^3, part of the left mandible with M$_3$, and an astragalus (AMNH 109521 [cast]) (see Cifelli et al., 1989:fig. 5). No additional specimens from Bayan Ulan can be securely assigned to this taxon.

Comments.—Originally two species of *Palaeostylops* were recognized from the Gashato Formation of Mongolia, *P. iturus* (the type species) and *P. macrodon* (Matthew and Granger, 1925; Matthew et al., 1929). The close relationship between Asian *Palaeostylops* and North American *Arctostylops* was recognized in the original description; based partly on this relationship, a Paleocene age for the Gashato fauna was cautiously advanced. Dashzeveg (1982a) regarded *Palaeostylops* as a junior synonym of *Arctostylops*, promoting an even tighter intercontinental biostratigraphic correlation. Cifelli et al. (1989) countered Dashzeveg's (1982a) proposal. Examination of specimens collected subsequent to CAE from Gashato, Nomogen, and Bayan Ulan led Cifelli et al. (1989) to conclude that differences in size and morphology between *P. iturus* and *P. macrodon* warranted separate generic recognition. They maintained the generic name *Palaeostylops* for *P. iturus* and named the new genus and combination *Gashatostylops macrodon* for "*P.*" *macrodon.*

Gashatostylops was proposed based on the holotype of "*Palaeostylops*" *macrodon* plus more recently collected material from Bayan Ulan, which contributes additional diagnostic information to the genus. According to Cifelli et al. (1989:15), *Gashatostylops macrodon* differs from *Palaeostylops iturus* "in having relatively enlarged upper and lower second molars; in having cuspules, variable in number and development, on the lingual cingula of upper molars; in the weakness or absence of a sulcus separating the lingual cusps of M^1; in the presence of two rather than three upper incisors; and in having a laterally constricted snout, with the dental arcade multiply curved."

Fig. 13.—*Prodinoceras xinjiangensis*, right P^2–M^3 (V11144) in occlusal (top) and buccal (bottom) views. The loose teeth are mounted on a plaster plate. Scale = 15 mm.

Given that a thorough taxonomic revision of this genus is beyond the scope of this study, we tentatively accept the new combination of Cifelli et al. (1989), despite its weak character support. For instance, the upper incisor condition and the lateral constriction of the snout are based on the single Bayan Ulan specimen (AMNH 109521) and cannot be evaluated for any of the Gashato specimens referred to *G. macrodon* (Cifelli et al., 1989), because the Gashato specimens do not have the rostrum preserved. This uncertainty leaves open the possibility that a third species is represented by AMNH 109521 at Bayan Ulan, which, if proven, may resurrect the validity of *Palaeostylops macrodon.*

Pantodonta Cope, 1873
Pastoralodon lacustris Chow and Qi, 1978

Specimens.—A skull and associated lower jaw containing most of the deciduous cheek teeth and the erupting first upper and lower molars (V11143).

Comments.—The referred specimen represents a young individual; its erupting first upper molars are similar to those of the holotype recovered from Nomogen, supporting its assignment to *Pastoralodon lacustris* (Wang Yuanqing, personal communication). Further study is being conducted by Wang Yuanqing.

Dinocerata Marsh, 1873
Uintatheriidae Flower, 1876
Prodinoceras xinjiangensis Zhai, 1978
(Fig. 13, 14)

Specimens.—Partial maxilla and isolated cheek teeth, including left P^2, P^4–M^3, right P^2–M^3, from the same individual (V11144; Fig. 13); the loose teeth were not held in the bone when collected and

are mounted on a plaster plate in their presumed original sequence. A left mandible with P₄–M₃ (V11145.1) and a right mandible with M₂–M₃ (V11145.2) are also referred to this taxon (Fig. 14).

Description.—P¹ is unknown. P² is much smaller than P³⁻⁴; its labial two cusps are only partly separated, and are transversely compressed (Fig. 13). The lingual cusp is the lowest of the tooth; the trigon basin is small and shallow. Cingula are little developed on any margin of the tooth. P³ and P⁴ are similar in size and shape. They are molariform in that the protocone, paracone, and metacone are present, and the paraloph and metaloph fully developed, connecting the paracone and metacone to the protocone respectively. The cusps and lophs border a triangular trigon basin. There is no trace of conules or of a hypocone. The anterior and posterior cingula descend lingually, but they do not meet; a lingual cingulum is absent. M¹ is slightly narrower than P⁴. The molars differ from P³⁻⁴ in having a distinct posterior shelf, at the lingual end of which sits a conical hypocone. The molars bear narrow labial cingula and paraconules. The paracone is much larger than the metacone and has a ridge extending posteriorly. The paracone and metacone are more deeply separated than on the premolars. M²⁻³ are considerably narrower posteriorly than anteriorly. M³ is larger than M². The lingual cingulum is weak on the molars.

The symphysis is strong but the mandibular ramus is relatively thin between P₁ and M₃ (Fig. 14). The mandible deepens rapidly from its tip to a point below the canine and remains nearly constant in depth through the posterior end of M₃. The absence of an inframandibular flange suggests that this specimen represents a female individual. A mental foramen occurs posteroventral to the canine on the labial side of the mandible. The incisors and P₁₋₂ are missing on both mandibles. The alveoli indicate a lower dental formula of 3–1–4–3. Judging from the cross section of its root, the canine is robust. The diastema measures 33 mm between the canine and P₁. P₄ is molariform. P₄–M₃ increase in size posteriorly and are similar in the following features: the paralophid and paraconid are reduced, resulting in a short trigonid that is nearly open anteriorly; the metalophid is strong and oblique, extending posterolingually from the protoconid to the metaconid; the metastylid is distinct, being posterolingual to the metaconid; the hypoconid is well developed, anteroposteriorly compressed, and distantly separated from the protoconid by a broad hypoflexid; the cristid obliqua is strong and runs anterolingually from the hypoconid to the metastylid. The hypoconulid and entoconulid on P₄–M₂ are indistinct, forming a curved ridge along the posterolingual edge of the tooth. There is no entoconid crest and the entoconid is weak. M₃ differs from the other lower teeth in its much longer talonid, on which the entoconid is prominent and connected to the hypoconulid by a short ridge. The massive hypoconulid sends a hypoconulid crest anteriorly, meeting the cristid obliqua. Measurements are given in Table 1.

Comments.—The upper and lower dentitions of this taxon have previously been referred to different species or even different genera. The upper cheek teeth (V11144) were considered to be *Pyrodon* sp. (Qi, 1979, 1987; Li and Ting, 1983) and *Prodinoceras* sp. (Russell and Zhai, 1987). These teeth are considerably larger than *Prodinoceras martyr* from Gashato. The talon shelf on the molars, particularly

M³, is well developed, bearing a conical hypocone more prominent than that of most species of *Prodinoceras* (Schoch and Lucas, 1985). In these respects, V11144 is nearly identical to *Prodinoceras xinjiangensis* from Xinjiang, leaving little question as to its taxonomic assignment.

The lower jaws (V11145.1–2) were previously assigned to *Mongolotherium efremovi* (Qi, 1979, 1987; Jiang, 1983; Li and Ting, 1983) because of resemblances in mandibular shape, crown morphology, and short diastema, and to *Prodinoceras martyr* for unspecified reasons (Russell and Zhai, 1987). Qi (1987), based on personal communication with McKenna, proposed *Prodinoceras efremovi* as a new combination. Qi (1980) mentioned *Mongolotherium* sp. from the Bayan Ulan beds, later citing it (Qi, 1987) as co-occurring with *Prodinoceras efremovi*, *Prodinoceras* sp., and *Pyrodon* sp. This suggests the possible occurrence of specimens validly assignable to *Mongolotherium* at Bayan Ulan, although such specimens are unknown to us. Comparing the M₃ of V11145 with that of *P. xinjiangensis*, which coexists with *Coryphodon dabuensis* in the early Eocene Dabu Formation, Xinjiang (Zhai, 1978), shows no significant differences. Given the similarity to the upper and lower teeth of the type specimens of *P. xinjiangensis*, we refer the Bayan Ulan specimens, although likely from different individuals, to the former species. Lacking firm evidence to the contrary, we consider *Prodinoceras xinjiangensis* to be the only dinoceratan occurring in the Bayan Ulan fauna.

Prodinoceras, a key taxon for correlation of the Asian Late Paleocene, is beset by many taxonomic problems. In recent reviews of this genus (Dashzeveg, 1982*b*; Schoch and Lucas, 1985), *Prodinoceras* was considered to be a senior subjective synonym of several other taxa from Asia and North America. We follow these authors in employing the generic name *Prodinoceras* and note the lack of a phylogenetic analysis for the species contained therein. Obviously, unifying numerous specimens previously assigned different generic designations under a single "genus" has biostratigraphic side effects.

Condylarthra Cope, 1881
Mesonychidae Cope, 1875
Pachyaena sp.
(Fig. 15)

Specimen.—A left M² (V11146, Fig. 15).

Description.—The tooth bears an anterior contact facet but no posterior one. Nevertheless, this specimen is certainly M², being
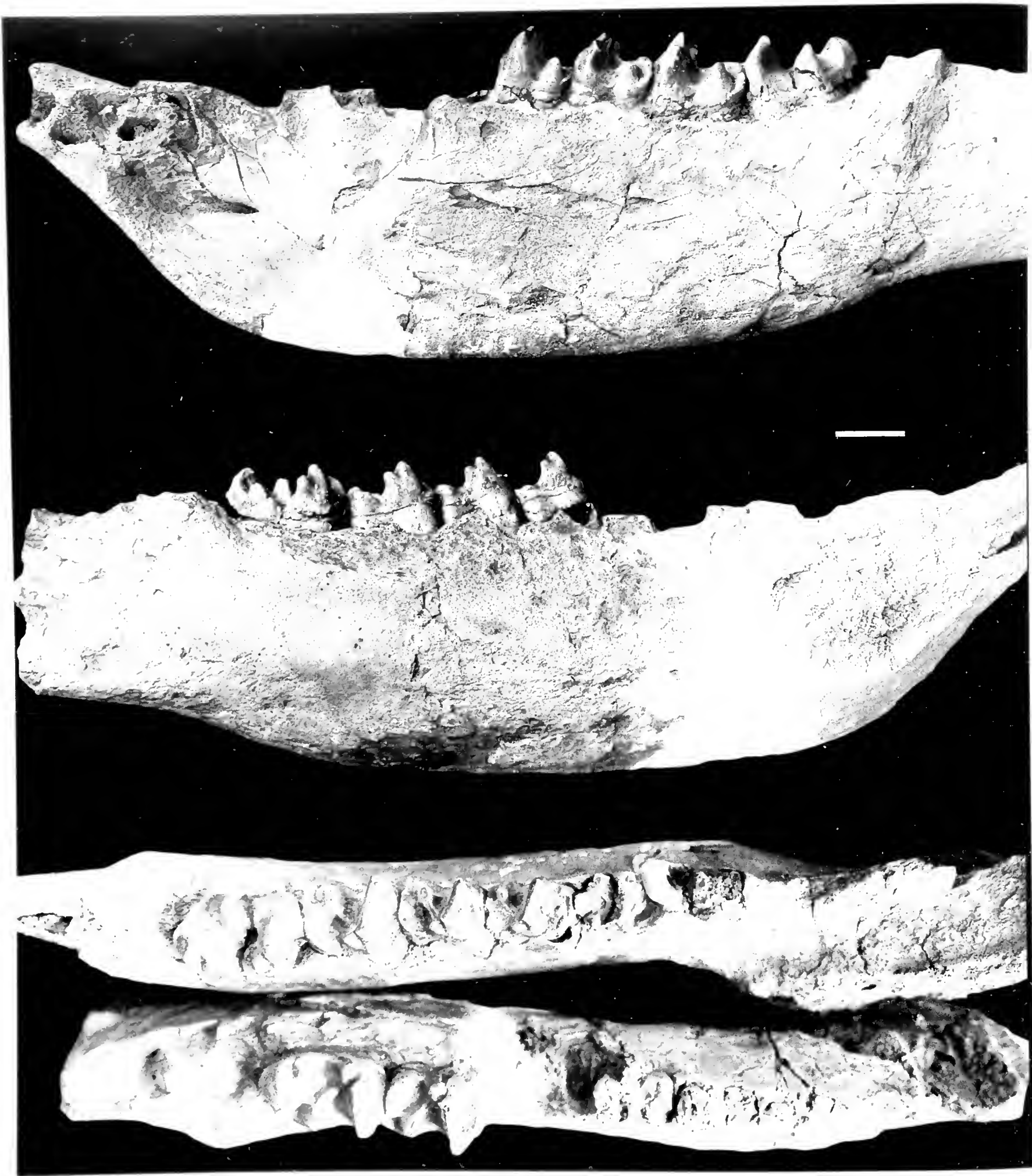
Fig. 14   *Prodinoceras angiangensis*, left (V11145.1) and right (V11145.2) mandibles. Buccal view of left mandible (top); lingual view of left mandible (middle); occlusal view of left and right mandibles (bottom). Scale = 10 mm.

comparable to those of North American species (Matthew, 1915; O'Leary and Rose, 1995). The tooth is large, measuring 21.2 mm long and 25 mm wide, but is substantially smaller than M¹ of *Pachyaena gigantea* from North America and slightly smaller than that of *P. gigantea* from Mongolia. The anterior, labial, and

posterior cingula are distinct. In crown view, the tooth is triangular in outline, with tips of the three cusps being slightly worn. Among the three cusps, which are all robust, the paracone is the most elevated. A wear facet on the anterolingual side of the paracone continues to the medial side of the parastyle. The me-

Table 1.—*Measurements (in mm; length, width) of specimens of* Prodinoceras xinjiangensis *Zhai, 1978.*

	P²	P³	P⁴	M¹	M²	M³
V11144	14.9, 13.4	17.0, 20.4	17.4, 21.2	18.6, 19.1	22.7, 24.3	24.5, 25.2
V11145.1			16.5, 13.7	17.6, 14.1	19.0, 17.9	28.4, 18.5
V11145.2					22.6, 18.0	28.4, 19.0

tacone is closely connected with the paracone, sharing the same base. A vertical groove separates these two cusps labially. The protocone, although lower than the paracone, is the most massive cusp; it is separated from the labial cusps by a longitudinal valley. The parastyle is broader than the metastyle; the latter is separated from the metacone by a narrow gap.

Comments.—Szalay and Gould (1966) argued that the large mesonychid, *Mesonyx obtusidens*, reported from the Naran Bulak beds of Mongolia (Gromova, 1952), actually belongs in *Pachyaena* because of its broad anterior, posterior, and labial cingula. Similar structures in V11146 enable us to assign it to *Pachyaena*, but given the limited material at hand, we are unable to allocate this single tooth at the species level.

Dissacus serratus (Chow and Qi, 1978)
new combination
(Fig. 16)

Plagiocristodon serratus Chow and Qi, 1978.
Dissacus sp. Chow and Qi, 1978.

Specimens.—V5480 (holotype), a fragmentary mandible with broken P_2, complete P_{3-4}, and broken M_1; V5478, a fragmentary maxilla with M^{1-3}; V5479, a fragmentary mandible with broken M_{2-3}; V11147, an isolated right P^3, a fragmentary left maxilla with M^{1-3}, a left mandible with trigonid of P_3 and P_4–M_2, and a right mandible with P_{3-4} and M_{2-3} (Fig. 16); the set of specimens (V11147) are associated with skeletal fragments from a single individual. Other specimens include two partial mandibles, each containing broken P_{3-4} (V11148.1 and V11148.2). Among these specimens, V5480 and

5478–9 are from the Nomogen fauna at Haliut; the rest from Bayan Ulan.

Revised Diagnosis.—A small species of *Dissacus* with lower premolar trigonids sharp and canted strongly posteriorly, trigonids and talonids equally wide, P_4 paraconid absent, and metaconid distinct on M_{1-3}. Differs from other species of the genus in having upper molar cusps less rounded, width of upper molars greater than length, M^3 considerably smaller and shorter than M^2.

Description.—The tricuspate P^3 is transversely compressed; it bears two labial cusps and one lingual (Fig. 16). The anterior labial cusp is larger than the posterior; the two are joined by a longitudinal crest which connects the anterior and posterior margins of the tooth. The small lingual cusp is supported by a separate root. The molar enamel is slightly worn. Weak cingula are developed on the labial, anterior, and posterior sides of the molars. The width of the upper molars is greater than the length. M^1 consists of three main cusps, the paracone being the highest and the protocone the lowest; there is no hypocone or conules. The paracone and metacone are conical and are separated by a narrow gap. The paracone is more labial than the metacone. Anterior to the paracone is a distinct parastyle. The protocone is concave labially; its base projects slightly anteriorly. The anterior surface of the tooth is gently concave, defined by the parastyle labially and the projected base of the protocone lingually. The trigon basin is shallow and broad. M^2 is the largest molar. The protocone is broken and, unlike M^1, its base does not project anteriorly. M^3 is considerably smaller than both M^1 and M^2, particularly in its anteroposterior dimension; the metacone is reduced, giving the tooth a triangular shape in crown outline.

V11147, preserving the symphysis through the anterior portion of the ascending ramus, represents the most nearly complete mandible available to us. The lower dental formula is ?–1–3–3. The mandible appears slightly deeper than that of the holotype (V5480) from Nomogen. Alveoli reveal that the canine was

Fig. 15.—*Pachyaena* sp., left M² (V11146) in occlusal (left), posterior (middle), and lingual (right) views. Scale = 10 mm.
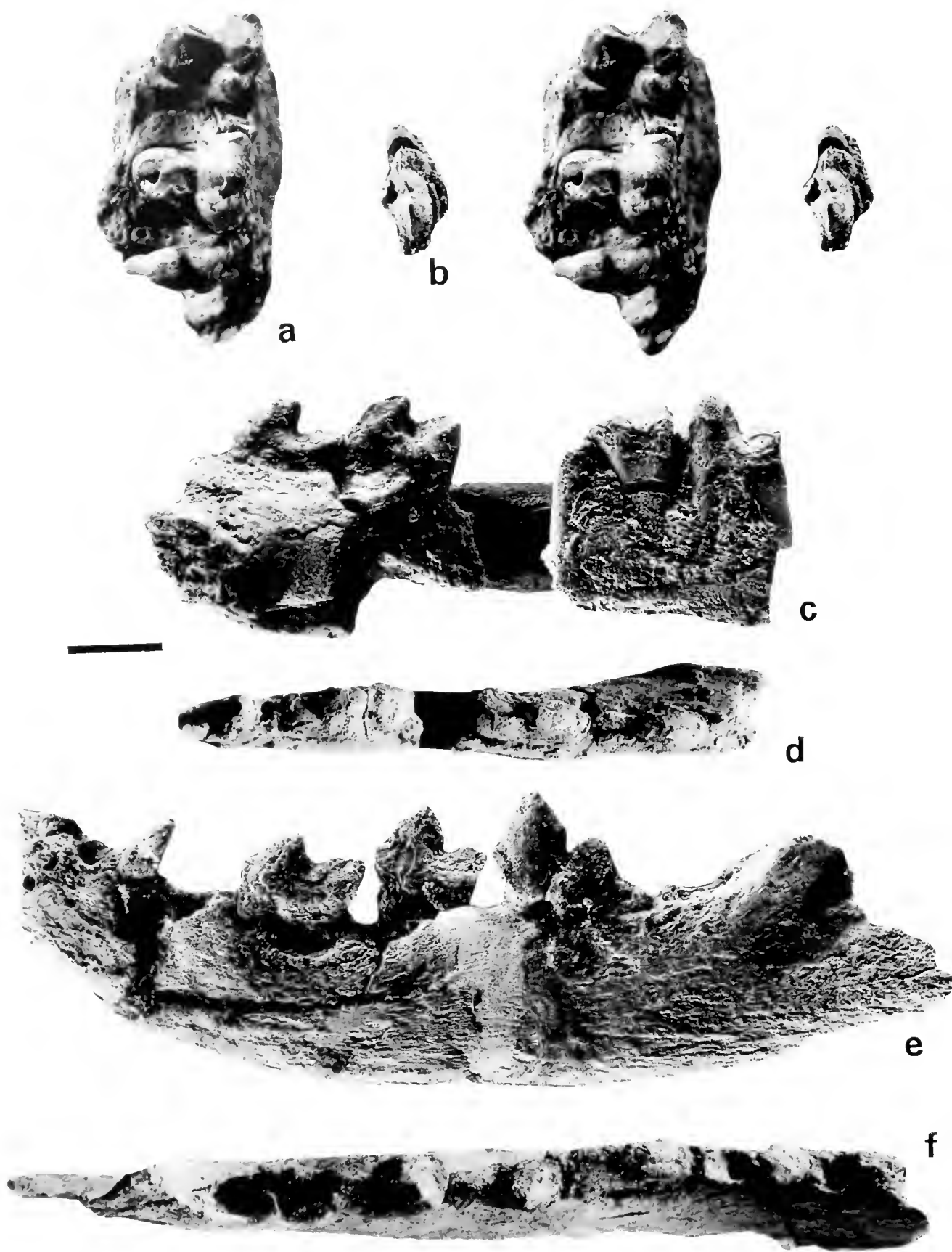
Fig. 16.—*Dissacus serratus*, n. comb. (V11147). a, b. Stereopairs of left M^{1-3} (a) and right P^3 (b) in occlusal view. c, d. Right mandible preserving P_{3-4} and M_{2-3} in lingual (c) and occlusal (d) views. e, f. Left mandible preserving trigonid of P_3 and P_4–M_2 in buccal (e) and occlusal (f) views. Scale = 10 mm.

strong and P_2 single-rooted (Fig. 16). P_{3-4} are similar in bearing a sharp, posteriorly canted anterior cusp and a long, trenchant talonid. M_1 has a high trigonid consisting of the protoconid and metaconid; unlike on P_4, the molar trigonid does not lean posteriorly. Like their upper counterparts, M_2 represents the largest, and M_3 the smallest, of the lower molars. On the molars, the protoconid and metaconid are appressed transversely, lending the protoconid a ridge-like form. The metaconid is distinctive and is slightly lower and more anteriorly placed than is the protoconid. The paraconid is vestigial. The talonid is represented by a sharp

longitudinal ridge extending posteriorly from the protoconid. The ridge occupies the labial portion of the tooth, aligning with the protoconid crest anteriorly. A small cusp on the lingual side of the hypoconid is probably the entoconid. The talonid basin is shallow lingual to the ridge.

Measurements of V11147 (in mm; length, width; * = estimated): P^3 8.1, 4.62; M^1 9.27, 9.55; M^2 8.94, 10.5; M^3 5.0, 8.3; P_3 (L) 8.8*, 3.72; P_4 (L) 10.9, 3.8; M_1 (L) 10.1, 4.6; M_2 (L) 11.3, 5.3; P_3 (R) 9.8, 3.67; P_4 (R) 11.1, 3.82; M_2 (R) 11.0*, 5.0*; M_3 (R) 9.33, 4.27.
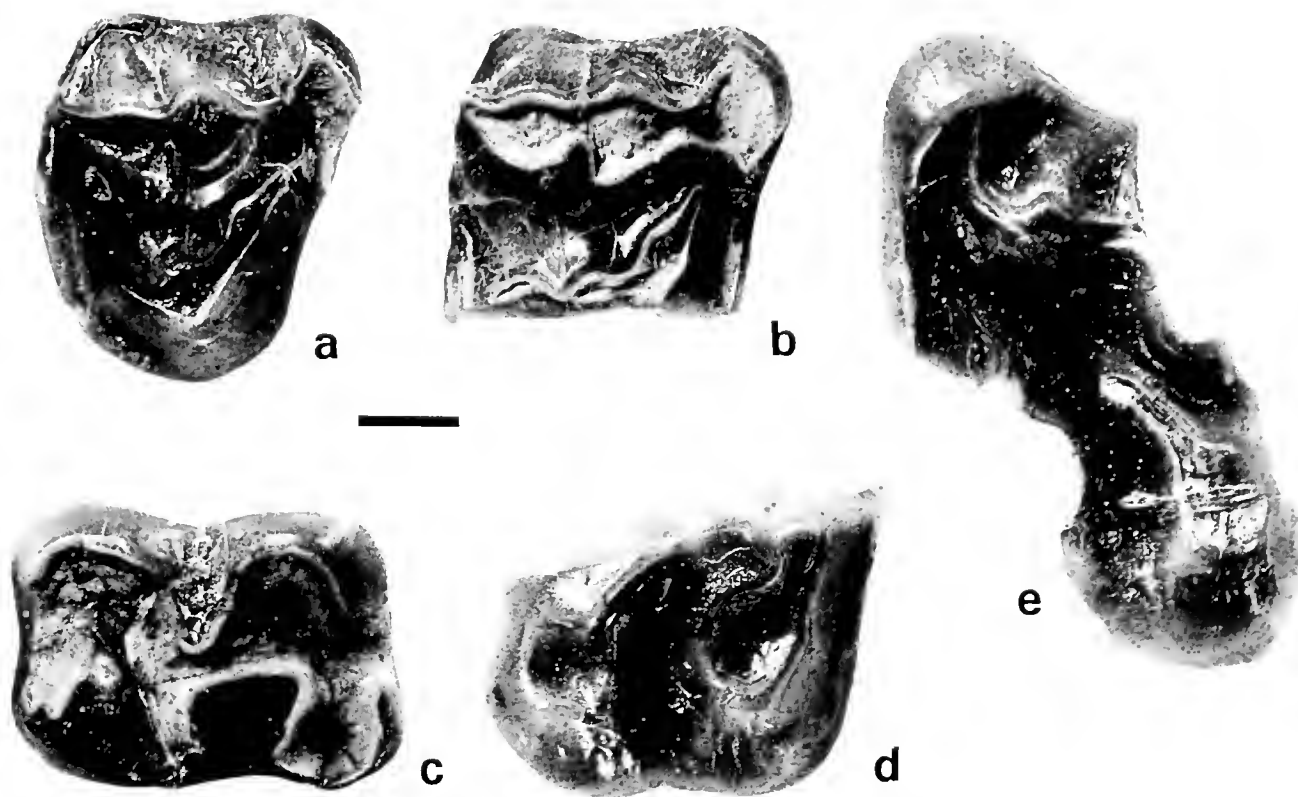
Fig. 17.—Perissodactyla, family indet., cheek teeth in occlusal view. a. Right P³ (V11149.3). b. Buccal half of right P⁴ (V11149.4). c. Right M₁ (V11149.6). d. Lingual half of right M¹ (V11149.5). e. Fragment of left M² or M³ (V11149.2). Scale = 2.5 mm.

Comments.—Two mesonychids were originally reported from the Nomogen fauna: *Plagiocristodon serratus* and ?*Dissacus* sp. (Chow and Qi, 1978:pl. 2, fig. 3). Qi (1987, personal communication with McKenna) has questioned whether the holotype of *Plagiocristodon serratus* (V5480) is a deciduous tooth of ?*Dissacus* sp. Ting and Li (1987), noting the similarities of size and talonid structure between *Plagiocristodon serratus* (V5480) and ?*Dissacus* sp. (V5479) from the Nomogen locality, queried whether these two forms may actually belong to the same species.

The upper and lower molars of a single individual from Bayan Ulan are indistinguishable from specimens attributed to ?*Dissacus* sp. from the Nomogen fauna at Haliut (Chow and Qi, 1978:pl. 2, fig. 1, 2). Moreover, P₃₋₄ of the Bayan Ulan specimens match those of the holotype of *Plagiocristodon serratus*. It seems likely, therefore, that the previous uncertainty surrounding the two taxa from Nomogen can be resolved with the Bayan Ulan material: all pertain to one species, as we consider them here. Consequently, we are confronted with the question: what name should be assigned to this taxon: *Plagiocristodon serratus* or *Dissacus serratus*? The answer must be based on a subjective judgment of whether the material from Nomogen and Bayan Ulan bear sufficient differences from *Dissacus* for recognition of the distinct genus *Plagiocristodon*. In comparison with Asian species of *Dissacus* (?*D. rotundus, D. magushanensis,* and *D. indigenus* [Wang,

1975; Dashzeveg, 1976; Yan and Tang, 1976]) and North American species (Matthew, 1915; O'Leary and Rose, 1995), we choose to use the new combination, because part of the material from Nomogen has been originally assigned to *Dissacus* and because the canted premolars in these specimens are an insufficient basis for a distinct genus. In fact, these features are common in other species of *Dissacus* (O'Leary and Rose, 1995).

Perissodactyla
Family indeterminate
(Fig. 17)

Specimens.—V11149.1, a left I³; V11149.2, a partial left M³⁽?²⁾; V11149.3, a right P³; V11149.4, a half right P⁴; V11149.5, a half right M¹; and V11149.6, a right M₁ (Fig. 17). All were collected from one small pit and, therefore, probably belong to a single individual, an inference corroborated by size compatibility and degree of dental wear.

Description.—I³ is chisel-shaped, with a convex labial surface and slightly wrinkled lingual surface. P³ bears two labial cusps which are confluent at their bases due to wear (Fig. 17). The paracone is larger than the metacone. A strong parastyle is anterolabial to the paracone. The preprotocrista is distinct, extending from the protocone toward the parastyle. The center of the preprotocrista is expanded, suggesting the presence of a paraconule. A short postprotocrista extends to the posterior side of the metacone. The lingual part of P⁴ is broken; still, it is clear that this tooth is larger than P³ and that P³⁻⁴ are similar in crown pattern. The anterior and posterior edges of P⁴ are parallel, giving the tooth a rectangular shape which suggests development of a

hypocone. Only the lingual half of the right M^1 is preserved, on which the well-developed hypocone is separated from the protocone by a broad but shallow valley. The strong preprotocrista extends anterolingually; a postprotocrista is absent. The hypocone is slightly smaller than the protocone and has a distinct ridge that runs anterolingually, becoming thinner and lower in the trigon basin. The left $M^{3(?2)}$ is broken anterolingually and posterolabially. This tooth is large, but its crown is quite low. Although broken, it is perceivable that the metacone is larger and located more lingually than the paracone; both cusps are connected by a centrocrista. The labial margin of the tooth appears to have a deep ectoflexus. The parastyle is as high as the paracone and connects with the latter by a low, curved ridge. The labial portion of the preprotocrista ends in a valley between the paracone and the parastyle. The hypocone is strong, likely smaller than the protocone. From the hypocone, a curved crest arcs anterolabially, tapering and diminishing in height along its course, into the broad trigon basin. The only lower tooth, a complete right M_1, is heavily worn. This tooth has a rectangular outline, with the trigonid and talonid subequal in size. The paraconid connects with the protoconid by a straight paracristid. The metaconid is larger and more lingually placed than the paraconid. The hypoconid and entoconid are large whereas the hypoconulid seems poorly developed. A strong cristid obliqua joins the trigonid slightly lingual to the midline of the tooth, resulting in a deep hypoflexid.

Comments.—These teeth, particularly M^3, are similar in size and crown morphology to *Lambdotherium*, but presence of a mesostyle on M^3 cannot be confirmed due to breakage. Nonetheless, these teeth were previously cited as ?*Lambdotherium* sp. (Jiang, 1983; Li and Ting, 1983; Russell and Zhai, 1987). These teeth, except the seemingly abnormally large M^3, have also been compared with *Hyracotherium*. However, the rectangular shape of the lower molar, more lingually extended cristid obliqua, poorly developed hypoconulid, and broadly separated protocone and hypocone in upper molars distinguish the Bayan Ulan form from early perissodactyls such as *Hyracotherium sandrae* from North America (Gingerich, 1989), *Orientolophus hengdongensis* from China (Ting, 1993), and European *Cymbalophus* (Hooker, 1980, 1984).

New material recently recovered from Wutu, Shangdong Province, China, sheds light on the identification of the Bayan Ulan material. A P^3 and a M^3 of a taxon closely similar to the Bayan Ulan form (Wang Jingwen, personal communication) show the same size variation, supporting the assumption that the Bayan Ulan specimens are from one species, probably from one individual. The complete M^3 from Wutu lacks a mesostyle, arguing against its reference to *Lambdotherium*. The Bayan Ulan and Wutu specimens probably represent a new taxon, but, other than their possible perissodactyl affinities, the fragmentary material precludes definitive taxonomic placement.

DISCUSSION

FAUNAL CORRELATION AND INTERCHANGE

Radioisotopic age control is unavailable for most of the early Tertiary mammal-bearing sequence of central Asia, the Bayan Ulan deposits included. Correlation of these faunas to the global geologic timescale depends primarily on biostratigraphic ties to the European and North American mammal-bearing sequences, both of the latter of which have various "absolute" age controls. Among the mainly endemic assemblages of the Mongolian Plateau, *Palaeostylops* and *Prodinoceras* have been singled out as "key" taxa linking the Gashatan mammal faunas of Mongolia to North American faunas. It was widely agreed that the Gashatan faunas are not older than Clarkforkian or younger than Wasatchian (Dashzeveg and McKenna, 1977; Gingerich and Rose, 1977; Rose, 1981), although correlation of these faunas to the lowermost Clarkforkian is also suggested (Dashzeveg, 1982*a*; 1988). Sloan (1987) has further estimated the timing of intercontinental migrations of dinoceratans and arctostylopids. In our view, however, these taxa are of limited bio-stratigraphic utility because of taxonomic uncertainties, as briefly discussed above, and the time-transgressive nature generally pertaining to faunal occurrences at an intercontinental scale (Gunnell et al., 1993). Correlations between individual Mongolian Paleogene faunas, such as the Bayan Ulan fauna, and North American or European biostratigraphic units based primarily on these two taxa, have advanced little over what was known during the early part of this century. While efforts to improve the geochronological database for the Asian early Tertiary are painstakingly being undertaken in several areas (McKenna, 1995; Emry et al., 1998; Lucas et al., 1998), another potentially profitable approach to improving intercontinental biostratigraphic correlation is to work out sequences of local faunas known from superpositional contexts in Asia, and then to correlate such sequences with those from other continents, as is being undertaken elsewhere (Meng and McKenna, 1996). Despite its pitfalls, however, mammalian biostratigrphy remains the most practical method of dating Tertiary sediments (Prothero, 1995). In this light, study of the Bayan Ulan fauna

furthers our understanding of faunal interchanges within Asia as well as between continents, and therefore enhances age estimates of Mongolian early Tertiary sediments based on biostratigraphic correlation.

As summarized in Figure 2, the Bayan Ulan fauna now consists of at least 24 taxa, which doubles the number of taxa compiled by Russell and Zhai (1987). Bayan Ulan taxa can be divided into three groups based on their biogeographic distributions. The first group consists of Asian endemics and includes *Pseudictops* and "eurymylids" (*Eomylus* and ?*Khaychina*). The second group includes taxa that are intercontinentally distributed at the generic or family levels: *Prodinoceras*, *Dissacus*, *Pachyaena*, *Prolimnocyon*, *Palaeostylops*, *Gashatostylops*, cf. *Viverravus* sp., ?leptictid, nyctitheriid, and *Tribosphenomys*. Those of the third group are intercontinentally distributed at higher taxonomic levels: *Lambdopsalis*, *Prionessus*, *Sarcodon*, *Hyracolestes*, *Pastoralodon*, and the possible perissodactyl. Apparently, group 2 taxa are most useful for biostratigraphic correlation.

Among Mongolian Paleogene faunas, the Bayan Ulan mammals show closest resemblance to those of the Naran Member of the Naran Bulak Formation, the lower member of the Gashato Formation, and the Nomogen Formation in sharing the following common taxa: *Pseudictops*, *Prionessus*, *Palaeostylops*, *Gashatostylops*, *Prodinoceras*, *Sarcodon*, *Hyracolestes*, *Pachyaena*, *Dissacus*, and "eurymylids" (Fig. 2). The Bayan Ulan fauna was previously regarded as slightly younger than the Nomogen fauna, and thus younger than the Gashato and Naran faunas as well (Qi, 1979; Chow and Zheng, 1980; Li and Ting, 1983). This assessment is largely based on the reported occurrence of the so-called ?*Lambdotherium* sp. and ?*Heptodon* sp. at Bayan Ulan (Qi, 1979; Jiang, 1983; Russell and Zhai, 1987). Withdrawing ?*Heptodon* sp. from the Bayan Ulan fauna, as suggested above, weakens this assessment. The occurrence of possible perissodactyl specimens and advanced features of *Prodinoceras xinjiangensis* relative to the species from the Gashato fauna are an insufficient basis to conclude that the Bayan Ulan fauna is younger than the Gashato, because the phylogenetic relationships of these two taxa are unclear and the occurrence of the perissodactyl specimens is uncertain. On the other hand, other faunal elements, such as *Sarcodon minor* and *Hyracolestes* sp., cf. *H. ermineus*, display features that appear to be more primitive than their Gashato relatives. Being incapable of differentiating

subzones at Bayan Ulan, we consider a single fauna to be represented, which correlates to the Gashato, Naran, and Nomogen faunas. The combination of these four local faunas forms the biotic basis for the Gashatan mammal age of the Mongolian Plateau (see Ting, 1998, and Wang et al., 1998, for more discussion on the Gashatan). These faunas are distinct from the Bumban fauna that is superpositionally above the Naran fauna and is characterized by the presence of *Hyopsodus*, *Gomphos*, *Homogalax*, *Hyracotherium*, and several ctenodactyloid rodents (Dashzeveg, 1988, 1990a; see Fig. 2).

Correlation of the Gashatan mammal age to the global geologic time scale depends primarily on mammals occurring in North American and central Asian faunas. The Bayan Ulan fauna adds the following ties to this intercontinental correlation.

Tribosphenomys

Rodents are widely regarded as having originated in Asia (see Krause and Maas, 1990), given, in part, the occurrence of their nearest known relatives, *Heomys orientalis* (Li, 1977; Dawson et al., 1984) and other "eurymylids," in the Paleocene of China. Until recently, the earliest Asian rodents were all referred to the Ctenodactyloidea of early Eocene age (Dawson et al., 1984; Li et al., 1989; Dashzeveg, 1990a). Slightly older rodents are known from North America, including Clarkforkian *Acritoparamys atavus* (Dawson et al., 1984; Korth, 1984, 1994) and a new taxon recently described (Dawson and Beard, 1996). Despite their slightly later first appearance, the early Eocene ctenodactyloids from Asia have been considered "the most primitive" rodents given their resemblance to *Heomys* (Dawson et al., 1984; Dashzeveg, 1990a). Recent discoveries of *Alagomys* and *Tribosphenomys* in Asia (Dashzeveg, 1990b; Meng et al., 1994; Tong and Dawson, 1995) and *Alagomys* in North America (Dawson and Beard, 1996) have significantly altered phylogenetic interpretations of gliriform mammals, while continuing to underscore a probable Asian origin of the Rodentia. The importance of these new forms comes from the fact that *Alagomys* is the only taxonomically unambiguous gliriform shared by Mongolia and North America near the Paleocene–Eocene boundary and that alagomyids bear centrally on the evolution and phylogeny of rodents and their early relatives. These new forms document a basal clade distinct from the conventional Rodentia represented by paramyids and ctenodactyloids (Meng and Wyss, 1994; Meng et al., 1994; Dawson and Beard, 1996). Their discovery narrows the morpho-

logical gap between gliriform and nongliriform eutherians and casts new light on the geographic distribution of early gliriforms, including the late Paleocene dispersal of these diminutive mammals across eastern Asia and North America via Beringia (Dawson and Beard, 1996). Of the two genera in the family Alagomyidae, *Tribosphenomys* is more primitive than *Alagomys* in several features, such as a buccal shelf on P^3–M^3, a small paraconid on M$_1$ and M$_2$ in young individuals, and a large hypoconulid lobe on M$_3$ (Dawson and Beard, 1996). The nonmolariform P$_4$ in the new material of *Tribosphenomys* documented above adds another feature consistent with this observation. A new species of *Tribosphenomys* has recently been discovered from the same beds yielding *Alagomys inopinatus*, that is, the early Eocene Bumban Member of the Naran Bulak Formation, Nemegt Basin, Mongolia (Dashzeveg, personal communication). This species is more advanced than the type species of *Tribosphenomys* in lacking P^3. Therefore, morphologies of *Tribosphenomys* and *Alagomys* appear consistent with the relative age estimate that the Bayan Ulan fauna is older than that from the Bumban Member, and suggest correlation of Gashatan faunas with those of as early as, or even earlier than, the Clarkforkian NALMA.

Prolimnocyon

With regard to the origin of Hyaenodontidae, Africa and the Indian subcontinent have recently been postulated as potential geographic source areas, from which hyaenodontids—possibly derived from palaeoryctids (Mahboubi et al., 1986)—dispersed to North America through Asia (Gingerich, 1989; Gingerich and Deutsch, 1989; Krause and Maas, 1990). The earliest *Prolimnocyon* in North America occurs in the earliest Wasatchian, and therefore "it appears that *Prolimnocyon* is part of a hyaenodontid radiation that did not reach North America until Wa$_0$ time" (Gingerich, 1989:37). The discovery of *Prolimnocyon* at Bayan Ulan lends support to Gingerich's hypothesis and partial support to the African center of origin scenario. However, the possible late Paleocene creodonts from Morocco (Gheerbrant, 1995) are too fragmentary to be diagnostic, and a link between early Tertiary hyaenodontids from Asia and Africa has yet to be established. The Bayan Ulan material introduces a new wrinkle in the consideration of hyaenodontid origins. The close similarity between the Bayan Ulan form and North American taxa suggests that hyaenodontids participated in an Asian and North American faunal ex-

change occurring near the Clarkforkia/Wasatchian transition. The primitive features of *Prolimnocyon chowi* compared with early Wasatchian species of the genus from North America are consistent with the pre-Wasatchian age estimate we favor for the Bayan Ulan fauna.

Prodinoceras *and* Palaeostylops

Dashzeveg (1988) concurred with Gingerich and Rose's (1977) suggestion that the dispersals of *Prodinoceras* and *Palaeostylops* are best interpreted as from North America to Asia, because their oldest representatives are known from the late Tiffanian and the early Clarkforkian of North America. To the contrary, phylogenetic analyses of Arctostylopidae (Cifelli et al., 1989) and *Prodinoceras* (Schoch and Lucas, 1985) suggest that the earliest diverging members of Dinocerata and Arctostylopidae are likely Asian, indicating possible dispersal of these taxa in the opposite direction. Regardless of the dispersal directions, *Prodinoceras* and *Palaeostylops* were traditionally used to establish the Clarkforkian–Gashatan intercontinental correlation, which, as shown above, is problematic. *Prodinoceras*, as construed by Schoch and Lucas (1985), ranges from the late Paleocene to the early Eocene, making faunal correlations using *Prodinoceras* coarser than previously believed. Similarly, North American *Arctostylops*—a *Palaeostylops* relative—occurs in North America not only in the Clarkforkian but also in the Tiffanian (Cifelli et al., 1989; Stucky, 1992), which, again, allows only rough correlation at best.

Pachyaena *and* Dissacus

The first appearance of *Pachyaena* in North America is at Wa$_0$ (Gingerich, 1989). In Mongolia, *Pachyaena* is also reported from the Naran fauna (Dashzeveg, 1988), but details of the morphology of the Naran form are unknown to us. *Dissacus* has a broader temporal distribution: from the middle Paleocene to the early Eocene (O'Leary and Rose, 1995; Zhou et al., 1995). The temporal distribution of this genus may be extended into the early Paleocene according to new calibration of the NALMA sequence (Woodburne and Swisher, 1995). Other Asian species of *Dissacus* span from middle to late Paleocene (Li and Ting, 1983; Dashzeveg, 1988).

Cf. Viverravus *Sp.*

The specimen from Bayan Ulan is the earliest record of viverravids on the Mongolian Plateau, documenting a northern range extension for Paleocene carnivorans in Asia, which were previously

known only from South China (Qiu and Li, 1977; Wang, 1978).

Nyctitheriidae

Due to its incompleteness, a thorough comparison of the Bayan Ulan form is impossible at present. What is known suggests that *Bayanulanius tenuis* compares most closely with North American *Leptacodon* and Asian *Bumbanius* and *Oedolius*. The new Bayan Ulan nyctithere supports Russell and Dashzeveg's (1986:290) contention that "insectivores from the early Eocene of Mongolia do not show signs of particularly strong endemism. Quite the contrary, they uniformly indicate a relationship to North American late Cretaceous or late Paleocene forms. "The Bayan Ulan taxon indicates that this pattern was established by at least Gashatan time in Asia.

Summary

The taxa listed above stand in combination most favorably for a Clarkforkian–Gashatan correlation, probably reflecting the Interchange Event #1 at the Clarkforkian NALMA proposed by Woodburne and Swisher (1995). With new ^{40}Ar/^{39}Ar dating and biostratigraphic work, the Clarkforkian NALMA and the earliest Wasatchian NALMA are now both placed within the late Paleocene (Prothero, 1995; Woodburne and Swisher, 1995). Therefore, the Paleocene–Eocene boundary is located within the early Wasatchian, which is consistent with some biostratigraphic conclusions (e.g., Beard and Tabrum, 1991). Similarly, the Paleocene–Eocene boundary needs to be shifted relative to Asian mammal sequences as well. Conventionally, the Bumban fauna is regarded as earliest Eocene in age (Dashzeveg, 1982a, 1988; Russell and Zhai, 1987; Krause and Maas, 1990; Ting, 1998) and the Paleocene–Eocene boundary in Asia is placed at the Naran–Bumban transition (Dashzeveg, 1988). Given the biostratigraphic correlation with North American faunas advocated here, the Gashatan must remain late Paleocene, while the possibility that the Bumbanian is latest Paleocene should also be considered.

Taphonomy and Paleoecology

The Bayan Ulan locality promises new information bearing on several currently debated aspects of taphonomy and paleoecology. The main insights for such endeavors will be derived from studies of carnivorous mammal coprolites and possible raptorial bird pellets, which are common at Bayan Ulan. The significance of these materials comes from the fact that they record life activities related to several important groups of mammals during a critical interval of faunal evolution on the Mongolian Plateau. Acid preparation of these nodules has produced the following taxa: *Lambdopsalis*, *Prionessus*, *Eomylus*, ?*Khaychina*, *Tribosphenomys*, *Palaeostylops*, and several "insectivores," some of which are rarely, if ever, collected through surface prospecting. While further taphonomic and paleoecological investigations are sorely needed, we offer the following initial observations:

1) In contrast to late Paleocene and early Eocene faunas of North America and Europe, Mongolian faunas are characterized by the scarcity or absence of arboreal forms such as plesiadapiform and lemuriform primates and chiropterans, a pattern reflected again at Bayan Ulan. A large arboreal frugivore and insectivore faunal component has been used to suggest a forested environment (Rose, 1981; Gingerich, 1989; Stucky, 1992), with forest/woodland conditions being recently cited as prevailing during the late Paleocene and early Eocene in North America (e.g., Gunnell et al., 1995). Forested conditions in North America were gradually replaced by more open and arid conditions during the Eocene and Oligocene (see Janis, 1993), coincident with the extinction of many arboreal forms, including primates, by the late Chadronian NALMA (Stucky, 1992). Central Asia was believed to be part of a "woody savanna" during the middle Eocene (Wolfe, 1985; Leopold et al., 1992; Janis, 1993), the earliest such environment known anywhere—similar conditions did not exist in North America until the late Eocene. The absence of arboreal taxa in the Mongolian Paleocene, such as at Bayan Ulan, indicates that, if close-forested conditions ever existed during the early Tertiary on the Mongolian Plateau, they had probably given way to more open habitats by late Paleocene Gashatan time.

The Mongolian Plateau appears to have differed climatically from southern and coastal regions of China, where coal beds and/or arboreal mammals have been reported from the early Tertiary (Chow and Li, 1963, 1965; Russell and Zhai, 1987; Beard and Wang, 1991; Beard et al., 1994; Beard and Wang, 1995). Early Tertiary sediments on the Mongolian Plateau are exclusively red beds of lake deposits and light colored river-channel sandstones. Given such sedimentary and faunal differences, the Mongolian Plateau likely represented a paleozoological province distinguishable from that of South China during the Paleocene and Eocene.

2) Abundant preservation of coprolitic material reflects a low-energy depositional setting, in which animal scats and possible bird pellets could accumulate and become preserved intact. Wet climatic conditions and small grain size of the enclosing matrix have been cited as factors that facilitate preservation of fecal material (Edwards and Yatkola, 1974). However, the Bayan Ulan material was exposed to considerable degradation before being fossilized. For instance, grooves and burrows in some coprolites (Meng and Wyss, 1997) indicate utilization of mammalian dung by beetles, an activity rarely documented in the early Tertiary fossil record (Hunt et al., 1994; Chin and Gill, 1996). This evidence suggests that some Bayan Ulan fecal material was not buried immediately after being produced, and yet escaped complete degradation. In addition, bacterial decomposition of dung is also observed for the Bayan Ulan coprolites (Meng and Wyss, 1997).

3) The Bayan Ulan fauna includes at least two multituberculates and three gliriform eutherians, the broadest coexistence of such taxa known. The sympatry of these taxa provides a potential test of hypotheses concerning the extinction of multituberculates, some of which emphasize competition with eutherian herbivores such as rodents (Van Valen and Sloan, 1966; Clemens and Kielan-Jaworowska, 1979; Krause, 1986), while others look for predation (Landry, 1965, 1967; Ostrander, 1984). Unlike in North America, however, where restructuring of mammal communities may be partly attributed to the immigration of rodents, presumably from Asia (Krause, 1986; Krause and Maas, 1990), the ascendancy of rodents and the extinction of multituberculates in central Asia may relate to different factors (Hopson, 1967; Meng and Fox, 1995). The Bayan Ulan fecal material provides direct evidence for the activities of predation, but the fact that multituberculates and several eutherians, including gliriforms, were prey items does not seem to explain whether predation selectively caused multituberculate extinction.

4) The relative importance of carnivorous mammal scat (Mellett, 1974) and bird pellets (Andrews and Evans, 1983) as sources of microvertebrate fossil assemblages has been a matter of dispute. Andrews and Evans (1983) suggest that bones in carnivorous scat are so weakened during the digestive process that their likelihood of surviving fossilization is very low. Coprolites from the Bayan Ulan contradict this assertion, indicating that both modes of accumulation contribute importantly to the fossil record. Unlike the mode of preservation implied in the cited works, in which bones are released from the fecal material before being fossilized, the Bayan Ulan specimens demonstrate that remains of small mammals can be preserved in situ in scat or pellets which become entirely lithified. Some small bones and teeth encountered on the surface at Bayan Ulan are likely the secondary products of weathering of coprolites.

5) The Bayan Ulan fecal material provides a glimpse at information seldom seen in the fossil record: impressions and natural casts of mammal hair (Meng and Wyss, 1997). The hair is preserved in association with identifiable bony remains of several extinct mammal groups, including the multituberculate *Lambdopsalis*. The chalky matrix of the nodules, which is often extremely fine, is an ideal molding material documenting microstructures of the outer cuticle pattern of hair.

ACKNOWLEDGMENTS

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A PRELIMINARY REPORT ON THE EARLY EOCENE MAMMALS OF THE WUTU FAUNA, SHANDONG PROVINCE, CHINA

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ABSTRACT

About 30 taxa of mammals, representing 26 families in 15 orders, have been collected in the coal beds overlying the *Homogalax*-bearing beds of the Wutu Formation in the Wutu Basin of Changle County, Shandong Province, China. This fauna differs from other early Eocene faunas of Asia in having a rodent assemblage dominated by paramyids, a diversification of carpolestids (including taxa that are both the most primitive and the most derived in dental morphology), and in sharing most families with the Paleocene of North America.

Preliminary analysis suggests that mammalian exchanges between the Asian and North American continents occurred frequently during the Paleocene and early Eocene. Provincialism within China may explain why forerunners of the Wutu mammals are largely unknown in the Chinese Paleocene record.

INTRODUCTION

This is a preliminary report on the mammalian fauna known from the early Eocene of the Wutu Basin. One of the most important Paleogene sedimentary basins in China, the Wutu Basin lies about 170 km east of Jinan, the capital of Shandong Province (Fig. 1). The first fossil mammal to be discovered in this basin, *Homogalax wutuensis*, was found by Li and his colleagues from the Shandong Museum in 1962 and described by Chow and Li (1963). On the basis of this fossil mammal, the Wutu Formation has long been considered to be early Eocene in age (e.g., Li and Ting, 1983; Russell and Zhai, 1987). In the summer of 1981 Li Yuntong of the Chinese Academy of Geological Sciences collected some coryphodontids in the same fossiliferous beds at Laowanggou where Li had earlier collected *Homogalax wutuensis*. In 1990 Tong and Wang recovered fossil mammals from coal beds above the mudstones containing *Homogalax* and a coryphodontid at Laowanggou, and later found additional fossils in the same coal beds near Xishangtuan Village and County Mine. Approximately 30 taxa have now been collected; the Multituberculata, Primatomorpha, Rodentia, Palaeanodonta, and part of the Insectivora and Perissodactyla have been described, but most of fossils are still under preparation or have not yet been studied thoroughly. As the collection continues to grow, new taxa are added to the faunal list.

GEOLOGICAL SETTING

The Wutu Basin is a small sedimentary basin having a total thickness of Eocene sediments of about 1000 m. Nearly all of the Eocene beds are overlain by Pleistocene deposits, and the Tertiary sediments are limited in exposure. Laowanggou, northeast of Wutu Village, is the best outcrop area for the Eocene, but exposures are usually separated by Pleistocene deposits (see Russell and Zhai, 1987:fig. 36).

Several normal faults occur in the Laowanggou section (Fig. 2). An east–west fault brings Paleogene or Cretaceous red conglomerates into contact with the underlying Paleozoic limestones. The Wutu Formation, which is composed of sandstones, mudstones, marls, shales, and coal beds, is separated from the red conglomerates by a fault. *Homogalax wutuensis* was collected from a white mudstone in the middle part of the section; the other fossil mammals reported here were found in carbonaceous shales and coal beds in the upper part of the formation. The thickness of the Wutu formation in this section is about 500 m. The upper fossiliferous bed is separated from the *Homogalax* bed by unfossiliferous sandstones, mudstones, and marls up to about 200 m thick.
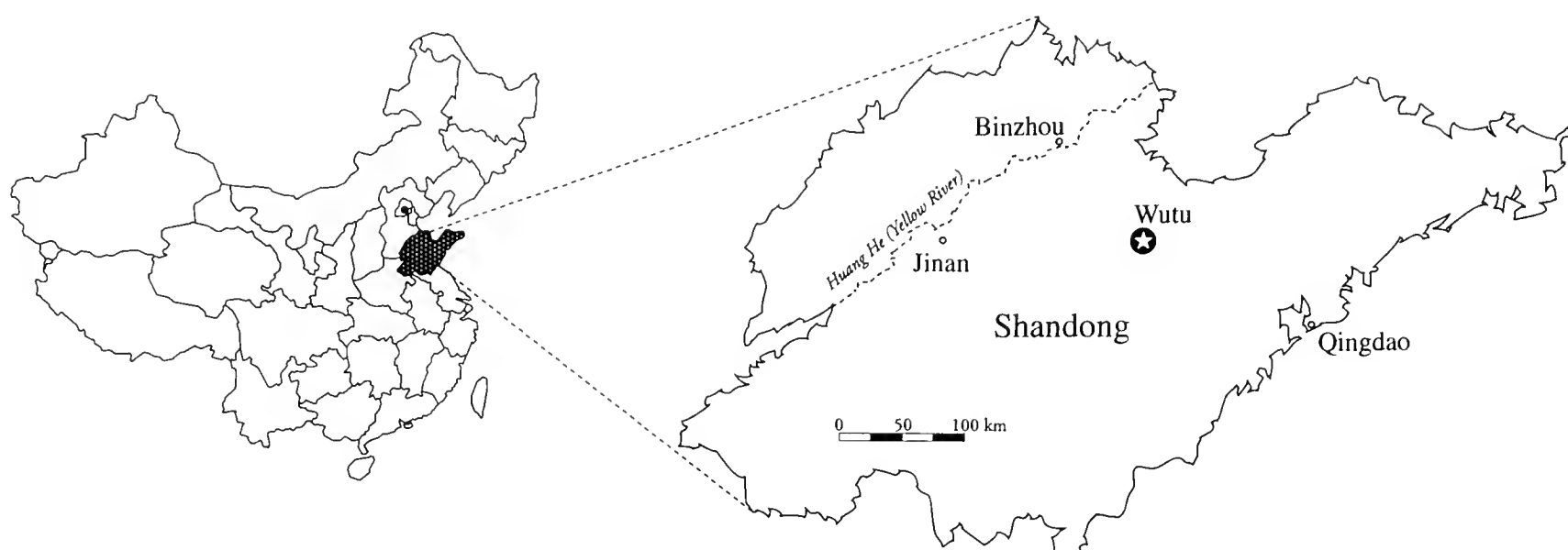
Fig. 1.—Map showing geographic position of the Wutu Basin (star) in Shandong Province, People's Republic of China.

The fossiliferous beds at Xishangtuan and County Mine can be correlated with the upper fossil beds in the Laowanggou section on the basis of both lithology and fossil mammals.

Following a concise overview of the mammals comprising the Wutu fauna, we will briefly discuss biogeographic and phylogenetic issues pertaining to this important Paleogene mammal fauna.

SYSTEMATIC PALEONTOLOGY

Order Multituberculata Cope, 1884
Neoplagiaulacidae Ameghino, 1890
Mesodmops dawsonae Tong and Wang, 1994
(Fig. 3A)

Comments.—This species shows many similarities to *Mesodma*, but it has a higher first serration on P_4, M_1 is more reduced relative to P_4, and P_3 is absent. *Mesodmops dawsonae* is the first ptilodontoid multituberculate to be reported from Asia. Its distinctions suggest that the family may be traced

back into the Paleocene of Asia (Tong and Wang, 1994).

Order ?Pholidota Weber, 1904
Suborder Palaeanodonta Matthew, 1918
Epoicotheriidae Simpson, 1927
Auroratherium sinense Tong and Wang, 1997
(Fig. 3B)

Comments.—This unusual species is comparable to *Amelotabes*, a Tiffanian palaeanodont from North
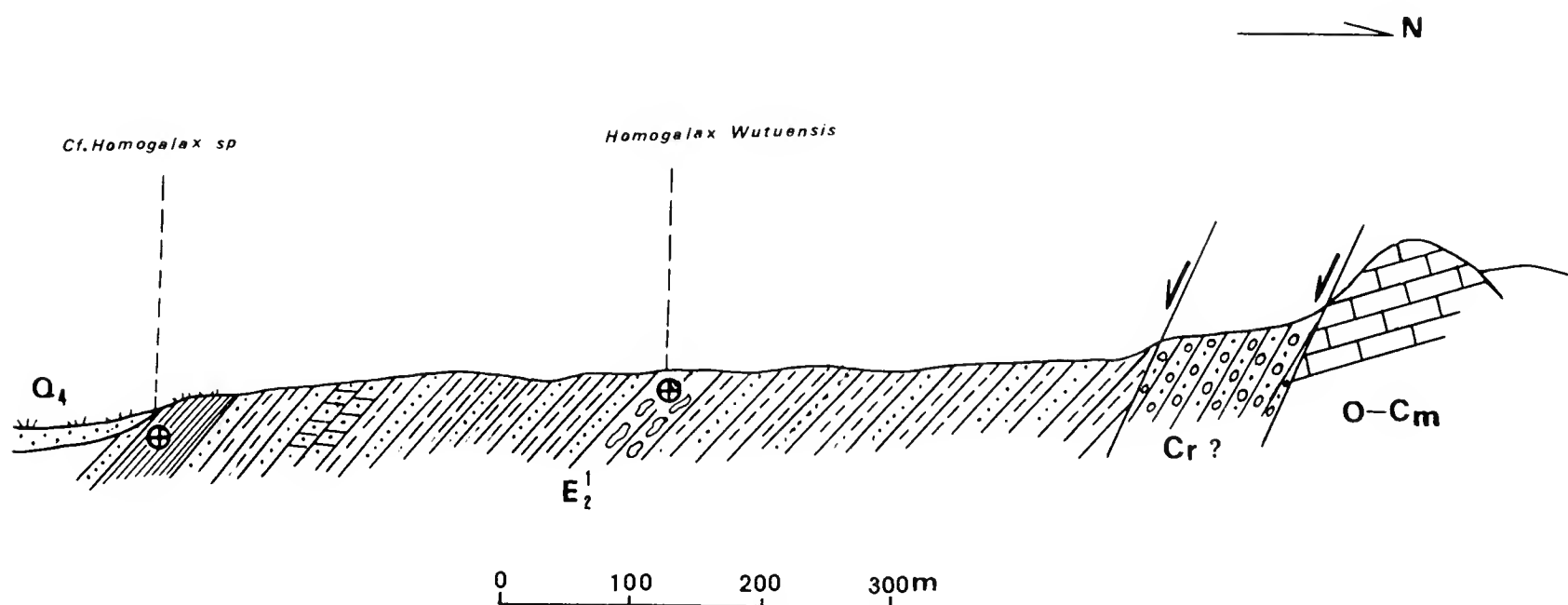
Fig. 2.—Stratigraphic section at Laowanggou in the Wutu Basin, showing position of fossiliferous beds there.
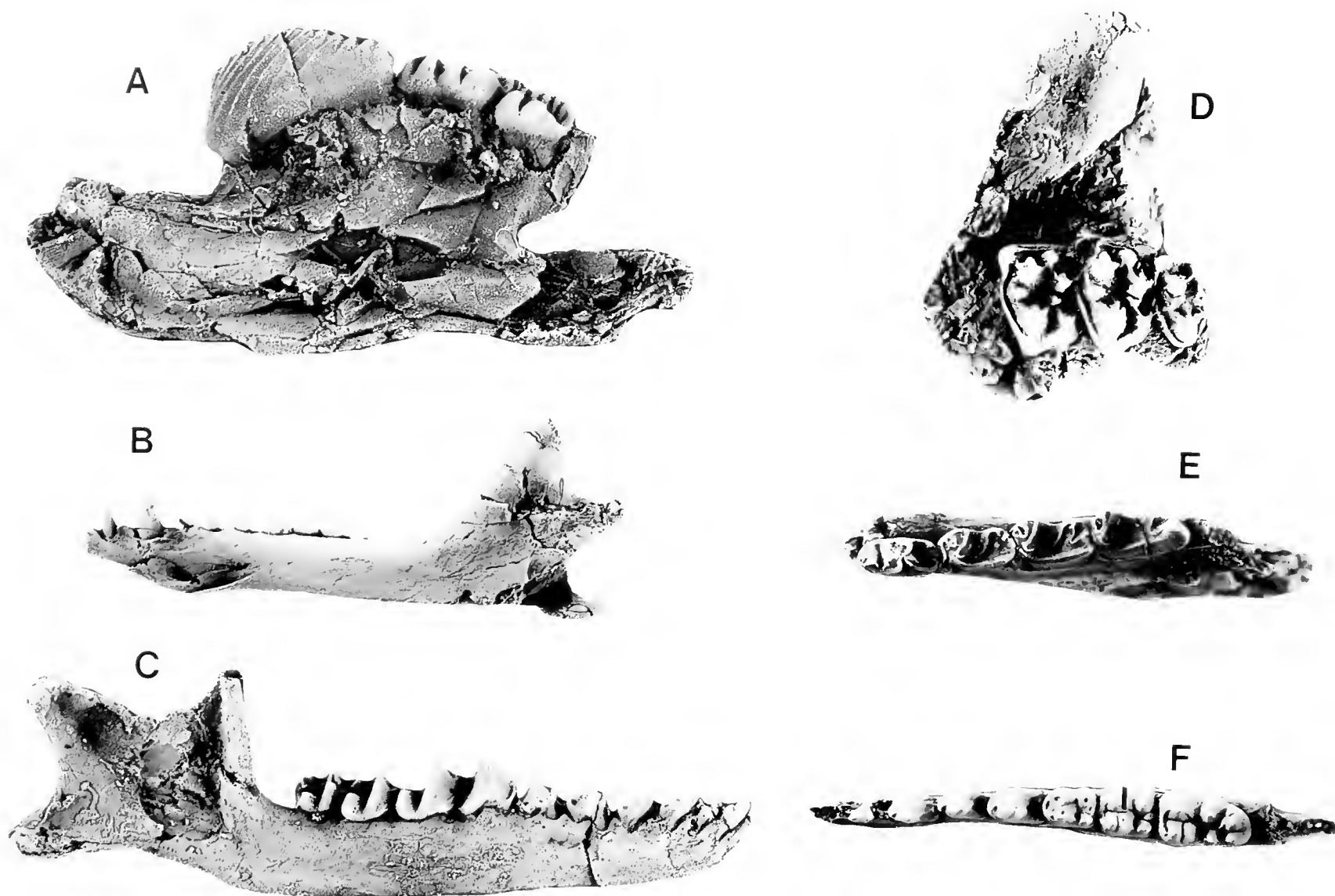
Fig. 3.—Selected fossil mammals of the Wutu Formation, Shandong Province, China. A. *Mesodmops dawsonae* Tong and Wang, 1994, IVPP V10699, holotype (part). Lingual view of right mandible (× 7). B. Epoicotheriidae, n. gen. and sp., IVPP V10703. Lateral view of right mandible (× 2). C. Erinaceidae, n. gen. and sp. (cf. *Litolestes*), IVPP V10709. Lateral view of right mandible (× 7). D. *Lophocion asiaticus* Wang and Tong, 1997 (cf. *Ectocion*), IVPP V10707. Occlusal view of left maxilla with M^{1-3} (× 2). E. Arctostylopidae, n. gen. and sp. (cf. *Arctostylops*), IVPP V10715. Occlusal view of left mandible with $P_4–M_3$ (× 2). F. ?Entelodontidae, n. gen. and sp., IVPP V10720. Occlusal view of right mandible with $P_1–M_3$ (× 2).

America (Rose, 1978), in the lower dental formula, reduced enamel, and cuspate postcanine dentition. The dental morphology of the Shandong form is, however, different from that of this Paleocene genus, and it differs from this and other North American epoicotheres in its basically fused molar roots. The upper postcanine dentition is similar to that of the Wasatchian *Alocodontulum atopum*, but less derived than the latter.

Order Proteutheria Romer, 1966
?Palaeoryctidae indeterminate

Comments.—A left lower molar with a high trigonid and lower talonid is questionably referred to this family.

Order Insectivora Illiger, 1811
Changlelestidae Tong and Wang, 1993
Changlelestes dissetiformis Tong and Wang, 1993

Comments.—This soricomorph is close to some nyctitheres, especially Paleocene *Leptacodon*, in

dental morphology. Even closer similarities are shared with the Asian Eocene soricomorph *Ernosorex jilinensis* (Wang and Li, 1990; Tong and Wang, 1993) in the construction of lower incisors and in having molars reduced in size from M_1 to M_3. The Asian genera allocated to the family Changlelestidae (*Changlelestes*, *Ernosorex*, *Tupaiodon*, and *Ictopidium*) differ from the Nyctitheriidae in having two reduced anterior premolars, and two large posterior premolars, and in the progressive reduction in size from M_1 to M_2. Changlelestids share some derived characters with plesiosoricids and soricids, suggesting the possibility of close affinities with extant soricomorphs.

New genus and species

Comments.—This new taxon should be compared to *Tupaiodon*. The specimens, including a fragmentary right maxilla with $C–M^2$ and some lower teeth, are similar to those of *Tupaiodon* and *Ictopidium*.

The three genera share the double-rooted upper canines, a marked difference in size between second and third premolars, distinct metastylar blades on P^{3-4} and M^1, distinct hypocones on P^4 and M^{1-2}, clear reduction in size from M_1 to M_3, and main cusps of cheek teeth sharper than those of known erinaceids. The new genus from Wutu differs from the other two genera in having conical hypocones, better developed conules, and distinct hypoconulids on the lower molars.

Erinaceidae Fischer de Waldheim, 1817
New genus and species
(Fig. 3C)

Comments.—This new taxon should be compared to *Litolestes*. The specimens are certainly erinaceids, and appear to be comparable to extant echinosoricines. Among the known Paleogene genera assignable to the Erinaceidae, the Wutu genus is closest to *Litolestes ignotus*, a late Tiffanian species from North America. Both genera share the derived characters of premolariform P_4 with a short talonid and greater decrease in molar size from M_1 to M_3. These two features appear to distinguish them from other Paleocene and Eocene taxa ascribed to the Erinaceidae by Krishtalka (1976) and Novacek et al. (1985).

?Nyctitheriidae
New genus and species

Comments.—This specimen, a skull with associated mandibles, seems to be similar to nyctitheriids in having the last premolar molariform, P^4 with a distinct hypocone, and trigonids of lower molars distinctly open. However, the upper canine is very long, and the molars decrease in size from M_1 to M_3, traits that distinguish the Wutu specimen from known nyctitheriids. If this taxon is a nyctitheriid, it is a very specialized one.

Order Anagalida Szalay and McKenna, 1971
Pseudictopidae Sulimski, 1968
New genus and species

Comments.—This specimen should be compared to *Haltictops*. A fragmentary right mandible with P_4–M_3 is morphologically close to *Haltictops*, which is known from the late Paleocene of the Nanxiong Basin, Guangdong Province. The Wutu specimen differs from *Haltictops* in having P_4 smaller relative to M_1, and anteroposteriorly compressed M_1 and M_2, and from *Pseudictops* of the latest Paleocene in its elongated talonid of M_3.

Mirorder Primatomorpha Beard, 1991
Superfamily Plesiadapoidea Trouessart, 1897
Carpolestidae Simpson, 1935
Chronolestes simul Beard and Wang, 1995

Comments.—*Chronolestes*, in which P^{3-4} are simple and P_4 lacks a polycuspidate blade-like structure, is a basal carpolestid that seemingly survived into the post-Paleocene. This Wutu carpolestid is more primitive in terms of dental morphology than *Elphidotarsius*, a middle Paleocene genus from North America. *Chronolestes simul* appears to be an Eocene survivor of a Paleocene carpolestid diversification in Asia, parallel to that of the North American continent. It indicates that mammalian exchange between North America and Asia took place during or before the Torrejonian, when *Elphidotarsius* made its first appearance in North America (Beard and Wang, 1995).

Carpocristes oriens Beard and Wang, 1995

Comments.—In strong contrast to *Chronolestes* (see above), *Carpocristes oriens* is the most advanced carpolestid. Among known North American species, the Tiffanian "*Carpodaptes*" *cygneus* and especially "*Carpodaptes*" *hobackensis*, both now referred to *Carpocristes* (Beard and Wang, 1995), are most similar to the Wutu species in the pattern of the last premolar, which is, nevertheless, less complicated than in *C. oriens*. *Carpocristes oriens* is probably related to the Paleocene carpolestid radiation of North America, and may reflect immigration into Asia in the post-Tiffanian.

Paromomyidae Simpson, 1940
cf. *Ignacius* **new species**

Comments.—A right mandible with P_4–M_2 and left M_{1-2} may be referable to *Ignacius*, based on relatively flat, low-crowned lower molars with shallow, basined talonid and a small P_4 relative to M_1. The new Wutu species is larger than *I. graybullianus*, which is the largest described species of the genus. There is a difference in molar shape, with the lower molars from Wutu more elongated anteroposteriorly and wider transversely than the known North American species.

?Micromomyidae Szalay, 1974
New genus and species

Comments.—This diminutive mammal, about the size of *Tinimomys*, should be compared to *Micromomys*. The taxon is represented by a right mandible with P_{3-4}, talonid of M_2, and M_3. Its affinities

with micromomyids are supported by P_4 with a remarkably hypertrophied trigonid and a low talonid. A notable difference from known micromomyids is in the trigonid of M_3, on which there is a well-developed paraconid and a relatively deep trigonid basin. Absence of a paracristid on the trigonid of P_4 is another difference from North American species.

Order Rodentia Bowdich, 1821
?Yuomyidae Dawson, Li, and Qi, 1984
Bandaomys zhonghuaensis Tong and Dawson, 1995

Comments.—A very small metacone on P^4 and a wider talonid than trigonid on P_4 suggest that this species of primitive ctenodactyloid may be near the base of the family Yuomyidae (Tong and Dawson, 1995). Potential relationships with the Mongolian Bumbanian ctenodactyloids described by Shevyreva (1989) and Dashzeveg (1990*a*) require further study.

Alagomyidae Dashzeveg, 1990
Alagomys oriensis Tong and Dawson, 1995

Comments.—The unusual Paleogene rodent *Alagomys* was first described by Dashzeveg (1990*b*) based on material from the Nemegt Basin of Mongolia. In the Nemegt specimens P^4 is nonmolariform, as in the Cocomyidae. *Alagomys oriensis* has a molariform P_4, which would not be expected were its P^4 (currently unknown) to resemble that of *A. inopinatus* (Tong and Dawson, 1995).

Paramyidae Miller and Gidley, 1918
Acritoparamys? wutui Tong and Dawson, 1995

Comments.—This rodent resembles *Acritoparamys atwateri* of North America in many features. These two species differ enough from the genotype, *A. francesi*, that the generic assignment must be re-examined.

Taishanomys changlensis Tong and Dawson, 1995

Comments.—*Taishanomys* has a deep lower jaw with a short diastema and masseteric fossa extending forward to below M_3; its lower cheek teeth have a long anterior cingulum, lingually separated from the metaconid. Assignment to the Paramyidae is based on the cuspate molars with the trigonid slightly compressed anteroposteriorly and a large talonid, with a poorly developed hypoconulid (Tong and Dawson, 1995).

Rodentia indeterminate

Comments.—A left mandibular fragment with incisor and dP_4 or P_4 cannot be assigned with certainty

to family. The first lower cheek tooth is somewhat similar to dP_4 of paramyids.

Order Creodonta Cope, 1875
Oxyaenidae Cope, 1877
Oxyaena? **new species**

Comments.—A fragmentary left maxilla with P^4–M^1 is questionably referred to *Oxyaena*. P^4 and M^1 have elongate metastyles, the protocone of P^4 has anterior and posterior wings, and the paracone and metacone on M^1 are partly connate while the protocone is reduced. This specimen may be a relatively primitive *Oxyaena*, as suggested by the little enlarged protocone on P^4 and the less elongate metastyle and unreduced protocone on M^1.

Order Carnivora Bowdich, 1821
Viverravidae Wortman and Matthew, 1899
cf. *Protictis* **new species**

Comments.—A flattened skull with mandibles represents a new viverravid. The Wutu specimen differs from *Viverravus* and *Didymictis*, which survived into the Eocene in North America and Europe, but is closer to the Paleocene genus *Protictis*. It differs from all other viverravids in having a paraconid that is slightly larger and higher than the metaconid on M_1, and is distinct from *Protictis* in having a reduced entoconid on M_1.

Order Tillodontia Marsh, 1875
Esthonychidae Cope, 1883
New genus and species

Comments.—This new taxon should be compared with *Esthonyx*. Several fragmentary maxillae and isolated upper teeth are referred here. I^3 is large; there is no marked diastema between I^3 and the canine, which is laterally compressed; P^2 is double rooted. P^{3-4} and M^{1-3} have the pattern typical of *Esthonyx*. However, in some details the Wutu tillodont differs from both *Esthonyx* and *Azygonyx*.

Order Acreodi Matthew, 1909
Mesonychidae Cope, 1875
Dissacus sp.

Comments.—This taxon is represented only by several isolated lower teeth.

Hapalodectidae Szalay and Gould, 1966
Hapalodectes **new species**

Comments.—*Hapalodectes* is represented by several species from the early Eocene of North America and Asia and by *H. serus* from the middle Eo-

cene Irdin Manha beds of Nei Mongol. The Wutu specimens resemble *H. leptognathus* and *H. hetangensis* in the presence of an accessory metaconid cusp on the lower molars. The Wutu species is slightly larger than *H. hetangensis*, but smaller than *H. leptognathus*.

<div align="center">

Order Condylarthra Cope 1881
Hyopsodontidae Trouessart, 1879
New genus and species
</div>

Comments.—The Wutu specimens are close to *Hyopsodus* from the Paleogene of North America and Europe but is distinguishable from them at the generic level. The Wutu taxon differs from *Hyopsodus* in having the cristid obliqua extend from hypoconid to metalophid on the lower molars, and in a relatively reduced molar paraconid, small entoconid, undeveloped hypocone, and M_3^3 distinctly smaller than the anterior molars.

<div align="center">

Phenacodontidae Cope, 1881
Lophocion asiaticus Wang and Tong, 1997.
(Fig. 3D)
</div>

Comments.—The Wutu specimens referred to this taxon, including two fragmentary maxillae with M^{1-3} and dP^{3-4}, should be compared to *Ectocion*. The Wutu species is similar in several features to *Ectocion*, but it can be separated from this North American genus in such details as a prominent crest that extends from the hypocone to the metaconule in the upper molars, which is less well developed in *Ectocion*.

<div align="center">

Order Pantodonta
Pastoralodontidae
Pastoralodon **new species**
</div>

Comments.—Several lower cheek teeth are comparable to those of *Pastoralodon lacustris* from the late Paleocene Nomogen Formation of Inner Mongolia.

<div align="center">

Order Notoungulata Roth, 1903
Arctostylopidae Schlosser, 1923
New genus and species
(Fig. 3E)
</div>

Comments.—Compared with the advanced genera in the family, *Arctostylops*, *Palaeostylops*, and *Gashatostylops*, the Wutu specimens are more similar to the North American *Arctostylops*. Like *Arctostylops*, the new taxon has a lingually shifted metaconid and a clear ectocingulum on P_4, and unreduced M_3. The Wutu arctostylopid differs from these three genera and from *Anatolostylops*, an early Eocene genus from the Turfan Basin, in having M^3 slightly longer than M^2 and with a persistent sulcus as on M^2, separating protocone from pseudohypocone.

<div align="center">

Order Perissodactyla
Isectolophidae Peterson, 1919
New genus and species
</div>

Comments.—The material referable to this new taxon was collected in the coal bed. It differs from known species of *Homogalax*, including *H. wutuensis* from the same basin, in having the metacone subequal to the paracone on P^{3-4}, more distinct paraconule and metaconule on the upper molars, and better developed metaconulid on the lower cheek teeth.

<div align="center">

?Lophialetidae Matthew and Granger, 1925
Ampholophus luensis Wang and Tong, 1996
</div>

Comments.—This medium-sized primitive tapiroid has *Homogalax*-like upper molars and *Schlosseria*-like P^3 and P^4. It is assigned questionably to the Lophialetidae on the basis of a continuous protoloph–metaloph loop (Wang and Tong, 1996).

<div align="center">

Eomoropidae Viret, 1958
New genus and species
</div>

Comments.—Two mandibles from the Wutu Formation are quite similar to *Eomoropus quadridentatus* in lower molar morphology, but the cristid obliqua of the lower molars does not connect to the metastylid and the hypoconulids are absent.

<div align="center">

Order Artiodactyla
?Entelodontidae Lydekker, 1883
New genus and species
(Fig. 3F)
</div>

Comments.—Diacodexeids are common artiodactyls in the early Eocene of North America and Europe, but the Wutu specimens are distinct from them. Compared to diacodexeids the lower cheek teeth of the Wutu artiodactyl are more bunodont, having low, blunt cusps on the lower molars, an inflated P_4, and an enlarged M_3. Its dental morphology is suggestive of entelodonts, which first appear in the middle Eocene of Asia.

DISCUSSION

Several features distinguish the Wutu mammalian fauna from other early Eocene faunas of Asia. These are: 1) the rodent assemblage is dominated by paramyids as in Clarkforkian–Wasatchian faunas of North America, whereas in other Asian localities primitive ctenodactyloids are more prevalent; 2) carpolestid plesiadapoids are remarkably diverse, including the most primitive and the most specialized taxa in terms of dental morphology; 3) most of the known families are also represented in Paleocene and early Eocene faunas of North America, and definite endemic taxa are few; 4) of particular interest is the abundance of the soricomorph insectivore, *Changlelestes dissetiformis*, which accounts for about 80% of the sample.

Asian Paleocene mammals have been considered to be mostly endemic (South China "Redbeds" Research Group, 1977), but the Wutu fauna adds to growing evidence that mammalian exchanges between Asia and North America took place during the Paleocene. More than 15 taxa in the Wutu fauna are closely related to North American Paleocene mammals, reflecting sporadic but persistent mammalian interchanges between the continents since the Torrejonian or earlier. Beard and Wang (1995) pointed out that there are at least two episodes of trans-Beringian dispersal for carpolestids during the Paleocene. In fact, the Wutu mammals indicate that mammalian exchanges between the northern continents occurred in each mammalian age of the Paleocene. The carpolestid *Chronolestes* is dentally more primitive than *Elphidotarsius*, which first appeared in the Torrejonian of North America; this evidence suggests the occurrence of mammalian exchanges during the Torrejonian or earlier. The Wutu neoplagiaulacid, *Mesodmops dawsonae*, is another example showing a dispersal event during the Torrejonian. *Mesodmops* and *Mimetodon* first appeared in the Torrejonian, possibly derived from the less specialized *Mesodma*, but then evolved in different directions. *Mimetodon* shows mainly increase in molar cusp number, whereas the Wutu species stresses chiefly its last premolar (Tong and Wang, 1994). Other Wutu mammals, such as *Changlelestes dissetiformis*, *Dissacus* sp., and cf. *Protictis* n. sp. appear to confirm mammalian exchanges during the Torrejonian or earlier (equivalent to the Shanghuan Age of Asia; see Tong et al., 1995).

Other evidence demonstrates that mammalian exchanges occurred on a larger scale in the Tiffanian and Clarkforkian (equivalent to the Nongshanian Age of Asia). Allied to the Wutu mammals, *Litolestes*, *Acritoparamys*, "*Carpodaptes*," *Ignacius*, *Ectocion*, *Coryphodon*, *Arctostylops*, and *Oxyaena* first appeared in North America at that time. Of these, arctostylopids and coryphodontids probably moved out of Asia, and a *Litolestes*-like erinaceid, derived carpolestids, *Ignacius*-like paromomyids, an *Ectocion*-like phenacodontid, and *Oxyaena*-like creodonts definitely or presumably migrated from the North American continent to Asia in the Late Paleocene.

Mammalian exchanges within the Holarctic (Asia, Europe, and North America) in the early Eocene, which have previously been demonstrated, are also documented by the Wutu fauna. The occurrence of an *Esthonyx*-like tillodont, *Hapalodectes*, *Hyopsodus*-like hyopsodontid, and *Homogalax*-like perissodactyl can be used to confirm early Eocene mammalian exchanges. These fossil mammals imply that the age of the Wutu fauna is probably equivalent to the Graybullian, although more taxa in the Wutu fauna are related to Paleocene forms of North America.

At present, Asian Paleocene ancestors are unknown for most of the Wutu mammals, except for some in endemic families such as the Pastoralodontidae and Pseudictopidae. This may result from provincialism within China during the Early Paleogene. At least two climatic provinces can be recognized in China during the Paleocene and early Eocene: semiarid/arid subtropical conditions prevailed in central and southern China (generally referred to hereafter as "South China"), while moister conditions typified eastern China. Most of the known Paleocene mammals of China are from the "Redbeds" of South China, including Guangdong, Jiangxi, Hunan, Anhui, Henan, and Shaanxi provinces. In these areas Paleocene strata contain abundant evaporites, such as salt-bearing and gypsiferous beds. *Ephedripites*, a xerophytic plant, dominates the fossil gymnosperm assemblage, and *Palibinia* is usually found in early Paleogene deposits of South China. These lines of evidence indicate that South China had a hot and dry climate during that time. Paleocene and early Eocene mammals from this area exhibit a relatively high degree of endemism, although similarities at the suprageneric level have been recognized with North American early Paleogene faunas. In contrast, in eastern China carbonaceous deposits such as coal beds and oil shales occur in the lower Paleogene. Hydrophytic broad-

leafed plants were present at this time in eastern China. Data on the palynoflora and sediments indicate that eastern China was a relatively moist area. The Wutu mammals clearly inhabited this humid, eastern biotic province of China. Although study of the Wutu mammals suggests that their Paleocene forerunners may have existed in Asia, Paleocene mammal fossils have not yet been recovered from the more humid biotic province of eastern China.

ACKNOWLEDGMENTS

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A PECULIAR MINUTE GLIRES (MAMMALIA) FROM THE EARLY EOCENE OF MONGOLIA

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ABSTRACT

A new genus and species from the Lower Eocene of Mongolia (Tsagan Khushu) documents a previously unknown family of Glires. The complete lower dentition of this minute animal is known (incisor, P_4–M_3). The molar pattern shows a strong trigonid with protoconid and metaconid canted forward; the talonid is anteroposteriorly compressed, and the sinusid is confluent with the mesoflexid. The reduced number of attritional facet directions and the stair-like aspect of the tooth row indicate that transverse movements were important during chewing, as in lagomorphs. The incisor enamel is two-layered with tangential enamel in the portio interna and radial enamel in the portio externa. The absence of Hunter-Schreger bands (HSB) is a fundamental difference from the incisor enamel of all other known mixodonts and rodents. Cenogram analysis suggests that the Tsagan Khushu mammalian fauna occupied a nonhumid woodland environment. This new family reinforces the morphological and taxonomic diversity of Glires near the beginning of the age of rodents.

INTRODUCTION

Discovered in 1964 by one of us (D.D.), the locality of Tsagan Khushu, Quarry 1 (Nemegt Basin, Mongolia) has yielded numerous fossil mammals, reptiles, and birds, and also small gastropods and ostracods. Fossils are found at the bottom of the Bumban Member, by excavating and screen washing lenses of yellow sandy gravel that conformably overlie the green clays which constitute the Naran Member of the Naran Bulak Formation. The stratigraphic profile of the Paleogene deposits at Tsagan Khushu is given in Russell and Zhai (1987:64). Numerous elements of the mammalian fauna have been described (Dashzeveg, 1977, 1979a, 1979b, 1990a, 1990b; Dashzeveg and McKenna, 1977; Russell and Dashzeveg, 1986; Dashzeveg et al., 1987; Dashzeveg and Russell, 1988; Shevyreva, 1989), and the faunal list given in Table 1 shows that it is one of the most diverse early Eocene

faunas known from Asia. Dashzeveg (1982, 1988) correlated this fauna with the Wasatchian of North America and the Ypresian of Europe.

In the Tsagan Khushu area there is another fossiliferous level (Quarry 2) which is situated lower in the section (below the Bumban Member). It yielded mainly larger mammals than those found in Quarry 1: *Archaeolambda planicanina*, *Coryphodon tsaganensis*, *Prodinoceras* sp., *Dissacus indigenus*, *Pachyaena nemegetica*, *Arctostylops macrodon*, *Eurymylus laticeps*. For Russell and Zhai (1987:65): "The time difference that separates them [the two levels] is as yet undetermined, but is probably slight."

All of the specimens described here are in the collections of the Institute of Geology at the Academy of Sciences of Mongolia (PSS and MA).

SYSTEMATIC PALEONTOLOGY

Glires Linnaeus, 1758
?Mixodontia Sych, 1971
Decipomyidae, **new family**

Type Genus.—*Decipomys*, n. gen.

Diagnosis.—Minute Glires with lower dental formula of 1–0–1–3. Shortened mandible with strong ventral masseteric crest ending anteriorly at the level of M_1. Diastema very short. One large mental foramen. Incisor strong and extending behind M_3. Enamel of incisor two-layered, without Hunter-Schreger bands; tangential enamel in portio interna, radial enamel in portio externa. Subisodonty in the tooth row, with high-crowned molars (bilateral subhypsodonty) and a bilophodont tooth pattern. Tooth row shows a stair-like profile in lateral view. Metaconids of all cheek teeth canted anteriorly. Tooth pattern simplified, without paraconid (variably present in M_1) and with reduced or absent anterior cingulids. Trigonids prominent, talonids anteroposteriorly compressed and flattened, reduced to a narrow hypolophid uniting hypoconid with entoconid. Posterior arms of protoconids well developed. Synclinids communicate with mesoflexids. Wear facets BB2 and LL3 present.

Decipomys, **new genus**

Type Species.—*Decipomys mongoliensis*, n. sp.

Diagnosis.—As for the family (currently monotypic).

Etymology.—Latin *decipere*, to deceive; and Greek *mys*, mouse.

Decipomys mongoliensis, **new species**
(Fig. 1–6, 8, 9; Table 2)

Holotype.—PSS 20 208, left dentary with P_4–M_3.

Referred Specimens.—PSS 20 213, right dentary fragment with M_{1-2}; PSS 20 203, left dentary fragment with M_{1-2}; PSS 20 201, right dentary fragment with dP_4–M_2; PSS 20 207, left dentary fragment with M_1.

Type Locality.—Tsagan Khushu, Quarry 1, Bumban Member, Naran Bulak Formation, Nemegt Basin, southern Mongolia (see Dashzeveg, 1982:277; Dashzeveg 1988:473; Russell and Zhai, 1987:63, 87).

Known Distribution.—Bumbanian, early Eocene of the Naran Bulak Formation, Nemegt Basin, southern Mongolia.

Diagnosis.—As for the genus (currently monotypic).

Table 1.—*Mammalian faunal list for Tsagan Khushu Quarry 1, Bumban Member, Naran Bulak Formation, Nemegt Basin, Mongolia (rodents revised by J.-L.H.).*

Order Lipotyphla
 Family Nyctitheriidae
  Bumbanius rarus Russell and Dashzeveg, 1986
  Oedolius perexiguus Russell and Dashzeveg, 1986
Order Proteutheria
 Family Palaeoryctidae
  Naranius infrequens Russell and Dashzeveg, 1986
  Tsaganius ambiguus Russell and Dashzeveg, 1986
Order Primates
 Family Omomyidae
  Altanius orlovi Dashzeveg and McKenna, 1977
Order Condylarthra
 Family Hyopsodontidae
  Hyopsodus orientalis Dashzeveg, 1977
Order Perissodactyla
 Family Equidae
  Hyracotherium gabuniai Dashzeveg, 1979
 Family Isectolophidae
  Homogalax namadicus Dashzeveg, 1979
Order Artiodactyla: indet.
Order Notoungulata
 Family Arctostylopidae
  Arctostylops n. sp.
Order Rodentia
 Family Alagomyidae
  Alagomys inopinatus Dashzeveg, 1990
 Family Ivanantoniidae
  Ivanantonia efremovi Shevyreva, 1989
 Family Cocomyidae
  Adolomys ameristus Shevyreva, 1989
  Tsagankhushumys deriphatus Shevyreva, 1989
  Sharomys singularis Dashzeveg, 1990
  Bumbanomys edestus Shevyreva, 1989
  ?Esesempomys centralasiae Shevyreva, 1989 (not seen)
Order Mixodontia
 Family Eurymylidae
  Eomylus zhigdensis Dashzeveg and Russell, 1989
  Zagmys insolitus Dashzeveg, Russell, and Flynn, 1987
 Family Rhombomylidae
  Rhombomylus sp., cf. *R. turpanensis* Zhai, 1978
 Family Decipomyidae
  Decipomys mongoliensis, n. gen. and sp.
Order Mimotonida
 Family Mimotonidae
  Gomphos elkema Shevyreva, 1975

Fig. 1–4.— 1. *Decipomys mongoliensis*, n. gen. and sp., holotype, PSS 20 208. Left dentary preserving P$_4$–M$_3$, lateral view, ×13. Tsagan Khushu, Quarry 1, Mongolia. 2. *Decipomys mongoliensis*, n. gen. and sp., holotype, PSS 20 208. Left dentary preserving P$_4$–M$_3$, oblique view of tooth row. ×20. 3. *Decipomys mongoliensis*, n. gen. and sp., PSS 20 213. Right dentary preserving M$_{1-2}$, occlusal view, ×27. Tsagan Khushu, Quarry 1, Mongolia. 4. *Decipomys mongoliensis*, n. gen. and sp., holotype, PSS 20 208. Left dentary preserving P$_4$–M$_3$, occlusal view. ×27.

Etymology.—After Mongolia.

Description.—In two specimens (PSS 20 203, PSS 20 208) the anterior and medial parts of the horizontal ramus of the jaw are preserved. The jaw is strong and high, and looks sciurognathous. The horizontal ramus is relatively thick and high. The diastema is very short (its length is less than the length of P_4–M_1) and not much curved, as is the case in most mixodonts. The highly bent incisor has a flattened inner wall and extends at least as far posteriorly as M_3, and probably behind this tooth. The ventral masseteric crest is well marked and strong, and its anterior tip extends forward below the posterior part of M_1. The mental foramen is quite large, and is situated relatively high, at the tip of the masseteric crest. It can be deduced that the masseter lateralis superficialis was a prominent muscle. There is no trace of an area for insertion of anterior masseter medialis. The root of the coronoid process is behind M_3, and probably the dorsal edge of the posterior ramus was inclined at about 45°. The elongated and well-marked symphysis ends at the level of the anterior part of P_4. In lateral view a chin process can be observed.

Compared with other Paleocene and early Eocene Glires, the dentary of *Decipomys* shows some advanced characters and looks modern in shape. The ventral masseteric crest extends forward below M_1; generally, the most common condition in primitive rodents and mixodonts is for this crest to extend below M_3. Also, the fact that the incisor extends posteriorly behind M_3 is another advanced character. The jaw also looks shortened and massive, with a horizontal ramus that is high and relatively thick. The single, large mental foramen (a large mental foramen occurs frequently in fossorial rodents) is also notable: most mixodonts have two foramina, and this is considered to be the primitive condition. On the other hand, the shortness of the diastema, the absence of a well-marked dorsal masseteric crest, and the very posterior position of the root of the coronoid process are notably primitive features.

When all of these points are considered, the dentary of *Decipomys* at first glance looks similar to those of such undoubted rodents as *Meliakrouniomys wilsoni* (Harris and Wood, 1969:fig. 1) and *Remys minimus* (Hartenberger, 1988:fig. 2–4). In particular, the development of the masseteric crest and the size and position of the mental foramen are the same. However, in both rodent genera the diastema is typically rodent-like in shape and proportions, the cheek-tooth pattern can be derived from a known rodent ancestor (see below), and the lateral profile of the tooth row is more horizontal and flat and lacks the stair-like profile observed in *Decipomys*.

One of us (T.M.) studied the incisor enamel ultrastructure of PSS 20 201, PSS 20 203, and PSS 20 207. Pieces 1–2 mm in length were removed from the mandibles and imbedded in artificial resin. Subsequently, they were sectioned radially and longitudinally (for technical description, see Flynn and Wahlert, 1978), ground and polished, and etched with 2N HCl to make morphological details visible. After rinsing and drying, they were sputter-coated with gold and investigated under the scanning electron microscope.

The incisor cross section is oval, with the anterior part narrower than the posterior. The enamel cover is somewhat asymmetrical, extending far laterally but much less so on the medial side (Fig. 11). This condition resembles that in such primitive rodents as *Paramys atavus*, *Paramys delicatus*, and *Leptotomus*. The maximum diameter of the incisors is 0.5 mm mediolaterally and 0.9 mm anteroposteriorly.

The enamel thickness is approximately 40 µm in all three specimens. Two distinct layers, the portio interna (PI) and portio

Table 2.—*Dimensions (in mm) of cheek teeth of specimens attributed to* Decipomys mongoliensis, *n. gen. and sp. Abbreviations: L, anteroposterior length; wa, anterior width (trigonid); wp, posterior width (talonid).*

	dP_4	P_4	M_1	M_2	M_3
PSS 20 208					
L		0.82	0.84	0.89	0.97
wa		0.53	0.72	0.81	—
wp		0.65	0.81	0.79	0.79
PSS 20 203					
L			0.81	0.93	
wa			0.71	0.75	
wp			0.81	0.85	
PSS 20 213					
L			0.79	0.96	
wa			0.71	0.74	
wp			0.75	0.83	
PSS 20 201					
L	0.70		0.88	0.91	
wa	0.45		0.76	0.81	
wp	0.51		0.75	0.81	
PSS 20 207					
L			0.87		
wa			0.70		
wp			0.75		

externa (PE), are present. The PE comprises about 35–45% of the total enamel thickness (Fig. 6).

The inner enamel (PI) is formed by parallel, nondecussating prisms that are oriented perpendicularly to the enamel–dentine junction (EDJ; inclination 0°). Prisms run straight from the EDJ to the outer surface as in radial enamel, but are about 45° laterally deviated. This enamel type is called tangential enamel (Koenigswald, 1980; Koenigswald and Clemens, 1992). The prisms are "dorsoventrally" flattened; they are about 3.5–4 µm wide and about 1.3–1.5 µm thick (PSS 20 207). Thick plates of interprismatic matrix (IPM) are intercalated between the horizontal prism layers. IPM crystallites run approximately 90° to prism direction. Because the IPM plates have nearly the same thickness as the prisms, it is difficult to distinguish between IPM and prisms in longitudinal section (Fig. 8); in cross section, prisms and IPM can easily be recognized, however (Fig. 6). The boundary between PI and PE runs almost parallel to the EDJ.

The PE is formed by radial enamel. At the boundary between PI and PE, the prisms simultaneously turn sharply toward the tip of the incisor (inclination 60–70°), maintaining their parallel orientation but now running radially without lateral deviation, toward the outer enamel surface. Prism cross sections are lancet-shaped. In the PE, IPM is slightly thinner than in the PI, and IPM crystallites are oriented perpendicularly to the EDJ (inclination 0°). IPM does not form plates, but anastomoses regularly between the prisms, appearing in cross sections as a net with prisms filling the meshes. A prismless external layer (PLEX) is lacking.

There are four jugal teeth which are interpreted as P_4–M_3 (Fig. 2–5). Specimen PSS 20 201 shows dP_4, but the anterior part of this tooth is damaged; on the only preserved M_3 (specimen PSS 20 208) the metaconid is broken.
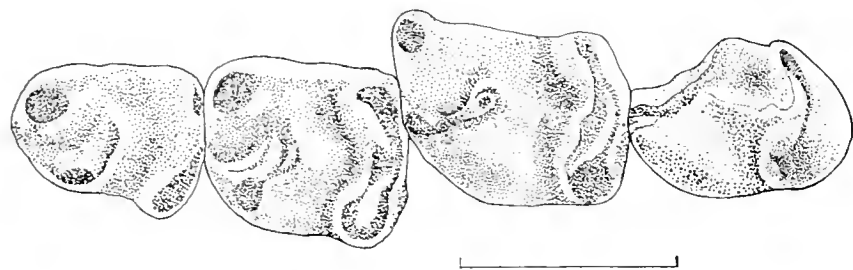
Fig. 5.—*Decipomys mongoliensis*, n. gen. and sp., holotype, PSS 20 208. Left dentary preserving P_4–M_3, occlusal view, ×27. Tsagan Khushu, Quarry 1, Mongolia. Scale bar = 1 mm.

The anterior part of P_4 is narrower than that of the other teeth, and therefore this tooth looks smaller than the molars. In the tooth row the M_2 must play a pivotal role, being a little larger than the other teeth. However, the dimensions and proportions of all of the cheek teeth are not very different and their crown pattern is almost the same, resulting in some sort of isodonty. This is a notable advanced character in comparison with other known contemporaneous rodents and mixodonts, for which the most frequent condition is a reduced premolar (P_4) and an elongated M_3, with trapezoidal M_1 and rectangular M_2.

In lateral view the crowns of the molars are relatively high (crown height of M_1 is equal to the width of this tooth), and this subhypsodonty is bilateral. The P_4 is more brachydont than the molars.

An important feature of the entire tooth row is its appearance in lateral view: it has a stair-like profile as occurs in some Mixodontia, and is comparable to that observed in modern Lagomorpha (Lopez Martinez, 1985:165). The trigonid, which is evidently higher than the talonid, constitutes an inclined wall with developed wear facets. The talonid is at the same level as the trigonid of the following tooth. We will discuss this point in more detail below as part of our discussion of wear facets and dental function.

The anterior part of dP_4 is damaged, and therefore it is not possible to recognize the precise pattern of the tooth. Apparently, the tooth was triangular with a reduced protoconid, indicating that the deciduous tooth was more reduced than the permanent P_4.

As is the case for the other cheek teeth, the prominent metaconid is the highest cusp on P_4. The anterior wall of the metaconid is vertical, so that this cusp appears to be canted anteriorly, and there is no trace of an anterior cingulum. The metaconid and protoconid are separated by an oblique and crescentiform notch. The protoconid has a posterior arm that constitutes an oblique crest extending over two-thirds of the labial side. The sinusid communicates with the mesoflexid, and in the deep valley that separates the trigonid from the talonid there is neither a mesoconid nor a mesostylid. A subvertical wear facet (facet BB2 + LL3b following the terminology of Butler, 1980; facet 1 following that of Crompton, 1971) occupies the wall of the posterior arm of the protoconid and the posterior part of the metaconid. The talonid is a thin ridge formed by the hypolophid which unites the entoconid and the hypoconid; it is lower than the trigonid.

The crown pattern of M_{1-2} is essentially similar. The specimen PSS 20 208 represents a younger animal; nevertheless, wear facets are well developed. On the anterior part of M_1 in this young specimen, it is difficult to determine whether an anterior cingulum with a minute paraconid is present or if the link visible in the anterior part of the tooth, in contact with and at the same level as the hypolophid of the anterior tooth, is due only to wear. Therefore, the occurrence of a minute paraconid on M_1 is ques-

tionable. As on P_4, the metaconids of M_{1-2} are sharp cusps that are also canted anteriorly. In lateral view the trigonid and talonid look asymmetrical in both proportion and wear: the trigonid constitutes two-thirds of the tooth and the metaconid + protoconid comprise a sharp cusp; the wear facet of the ridge of the entoconid–hypolophid–hypoconid is flat and forms a slightly concave hypolophid. A deep valley (sinusid + mesoflexid) separates the trigonid from the talonid and no accessory cusps are visible on either the buccal or lingual side. Due to the arrangement of the teeth, the posterior part of a tooth is at the same level as the anterior part of the following tooth, and in lateral view the tooth row has a stair-like profile. The bilateral hypsodonty of the teeth amplifies this effect.

Only a single M_3 is preserved, and the metaconid of this tooth is broken. The measurable length of M_3 is slightly longer than M_2 and M_1. No accessory cusp (no hypoconulid) is visible on the talonid.

Chewing Function and Wear Facets.—As noted by Butler (1985:fig. 4) the wear facets of the molars of primitive rodents differ from those of mixodonts, so that chewing must have been different in these two groups of Glires. At first glance, it appears that the wear facets of *Decipomys mongoliensis* are very similar to those of mixodonts (Fig. 11). In order to make accurate comparisons, we use the method first proposed by Butler (1980). As noted by Butler (1980:249), "molar teeth provide direct evidence of their functioning in the forms of attrition facets." Therefore, the direction of principal masticatory movements can be deduced from the study of wear facets. For this purpose, Butler (1952, 1973) had earlier proposed a nomenclature and enumeration scheme for dental wear facets. Crompton (1971) proposed a different enumeration scheme from that of Butler, and because Lopez Martinez (1985) followed Crompton's nomenclatural system, we give Crompton's enumeration in brackets. Following Butler's terminology, three kinds of facets can be distinguished on the molars of *Decipomys*: B–B facets made by buccal cusps of opposing teeth, producing wear facets 1 [2], 2 [1], 6 [3], and 7 [4]; L–L facets made by lingual cusps of opposing teeth, producing wear facets 4 [6], 3 [5], 9, and 8; and L–B facets made by lingual buccal cusp contacts (protoconid on hypocone or metaconule when hypocone is lacking, and hypoconid on protocone), producing wear facets 5 and 10 (no equivalent in Crompton's terminology).

The B–B and L–L facets result from the buccal phase, that is, when lower teeth are moving transversely, whereas L–B facets are generated during the lingual phase, when the lower teeth move obliquely forward.

In order to compare the molar wear facets of *Decipomys* and other early Glires, we drew the M_2s of several genera (same as those listed in character analysis table) with the camera lucida and noted the wear facets following Butler's (1980) terminology. As a first step in the study, the direction of the slopes for the visible facets was recorded on circular diagrams. This showed that the direction of most wear facets in the genera studied were very similar. Nevertheless, three differences did emerge: 1) the diversity of facets is lower in advanced mixodonts than it is in primitive mixodonts and primitive rodents; 2) wear facet 10 is subhorizontal in most rodents and in advanced mixodonts, but has a slope with an oblique direction in *Alagomys* and primitive mixodonts; 3) facets BB2 and LL2b (we refer to this facet as LL2b because of its more posterior position than facet LL2) are very marked in advanced mixodonts and *Decipomys*.

After comparison of both tooth patterns and wear facets, three groups of early Glires have been distinguished:
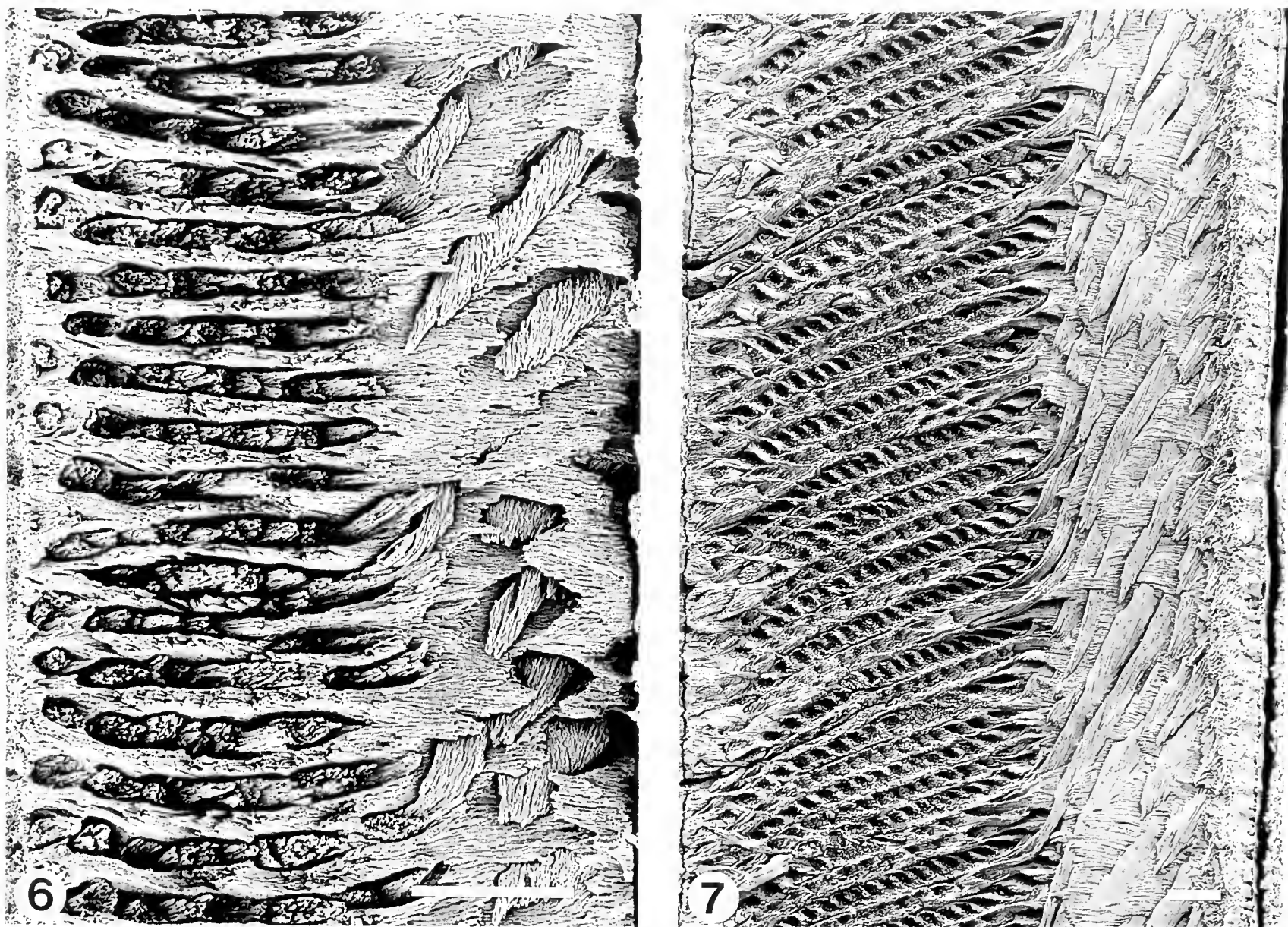
Fig. 6, 7.—6. *Decipomys mongoliensis*, n. gen. and sp., PSS 20 203. SEM micrograph of longitudinal section of lower incisor enamel. Tip of incisor is to the top and EDJ to the left. Enamel consists of two distinct layers. In the PI (left), single layers of parallel prisms alternate with thick, horizontal IPM plates, forming tangential enamel. Prisms are cut transversely (shown in cross section). The PE is formed by radial enamel in which prisms are inclined about 50° apically. IPM seems to form vertical plates, but anastomoses between the prisms. Scale bar = 10 μm. 7. *Anomalurus* sp., Recent, Central African Republic (MA 85). SEM micrograph of longitudinal section of lower incisor enamel. Tip of incisor is to the top and EDJ to the left. In contrast to that of *Decipomys mongoliensis*, the PI in rodents is formed by HSB, which are layers of decussating prisms. The uniserial enamel of *Anomalurus* superficially resembles the structure found in *Decipomys mongoliensis*, but these types of enamel are actually fundamentally different. In *Anomalurus* the PE consists of radial enamel like that of *Decipomys*. Scale bar = 10 μm.

1) A primitive group including *Alagomys* and primitive mixodonts (*Eomylus*, *Zagmys*, *Khaichina*). The trigonid is higher than the talonid with sharp cusps. Lateral wear facets are well developed (in particular facet 6 on the anterior wall of the hypoconid). From observation of wear facet 10 it can be deduced that the hypoconid trajectory onto the protocone is mainly linear and oblique in direction.

2) A "sciurid" group including *Sharomys*, *Paramys*, *Tamquammys*, and, to a lesser degree, *Ivanantonia*. Wear facets are relatively diverse. Main facets are 5 and 10 (made by lingual–buccal contacts) so the lingual phase with an oblique and forward movement predominates. In *Ivanantonia* the movement was almost anteroposterior (propalinal movement).

3) A *Mimotona* group including *Heomys*, *Gomphos*, *Eurymylus*, and *Decipomys*. The trigonid is higher than the talonid and there is an important facet LL2 and BB3b on its posterior side. In *Mimotona* the two facets form a continuum. In advanced mixodonts the buccal phase can be considered as important as the lingual phase, and the preeminent movement of the hypoconid

onto the protocone is transverse (ectental movement). This is not far from what is observed in Lagomorpha (a notable difference is that the anteroposterior movement is very reduced in lagomorphs). As observed by Lopez Martinez (1985), in lagomorphs one of the strongest facets is facet 2 (numbered 1 in her paper following Crompton's terminology). Lagomorphs are anisognath and alternatively grind from side to side (from without inwards). Without adequate material we cannot determine definitively whether or not this was also the case for some mixodonts, but many of them (*Eurymylus*, *Mimotona*, and *Decipomys*) show the same stair-like profile of the tooth row in labial view. Because the symphysis is important in *Decipomys*, the two rami must have been well fused: this also suggests one-sided movement in chewing (Weijs, 1975). The transverse component of movements during mastication was clearly important in advanced mixodonts (*Rhombomylus*, *Gomphos*, *Mimotona*, *Heomys*, *Decipomys*) but differed from that of modern lagomorphs in also having an anteroposterior phase. Anisognathy may well have occurred in these advanced mixodonts. As noted above, the characteristic
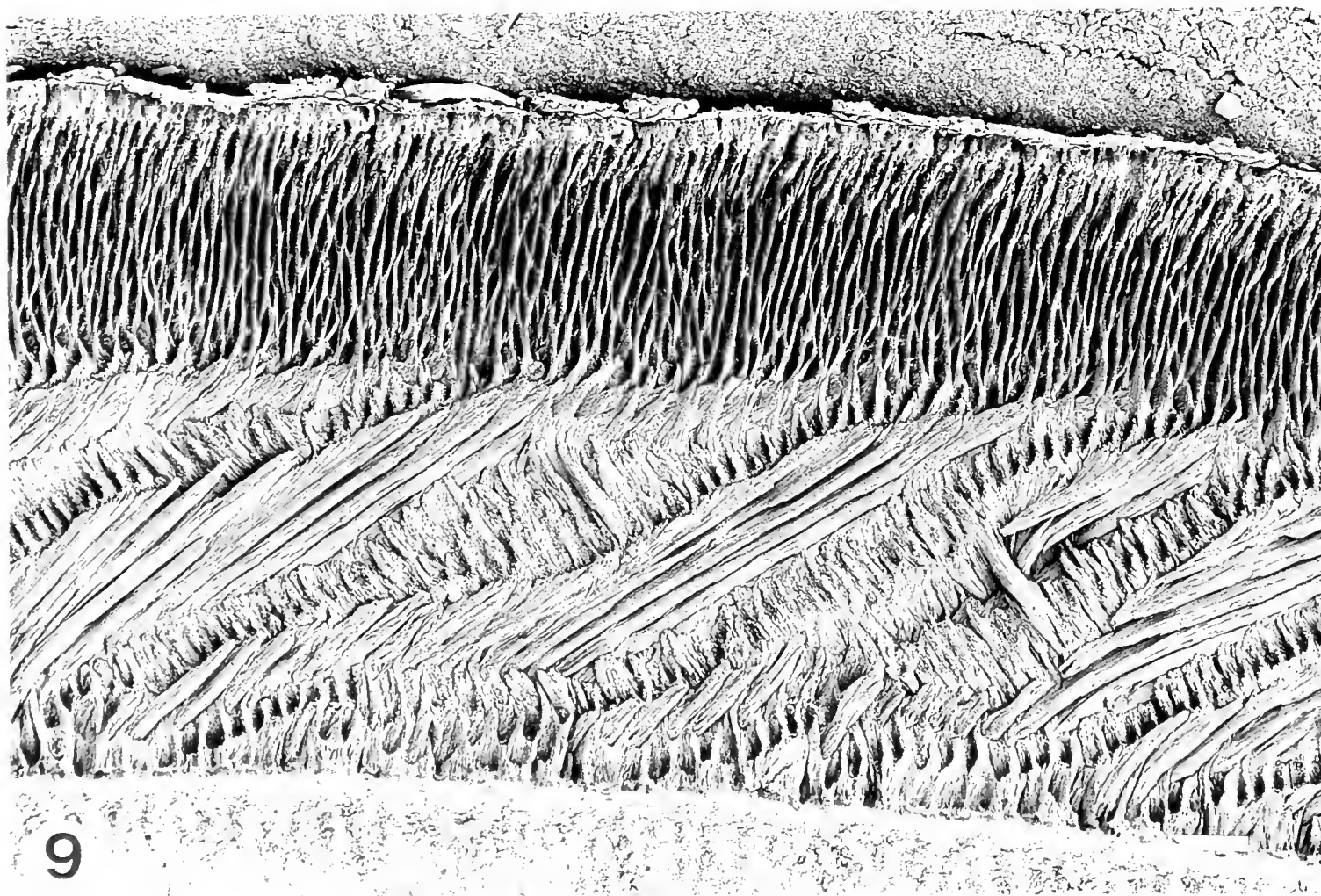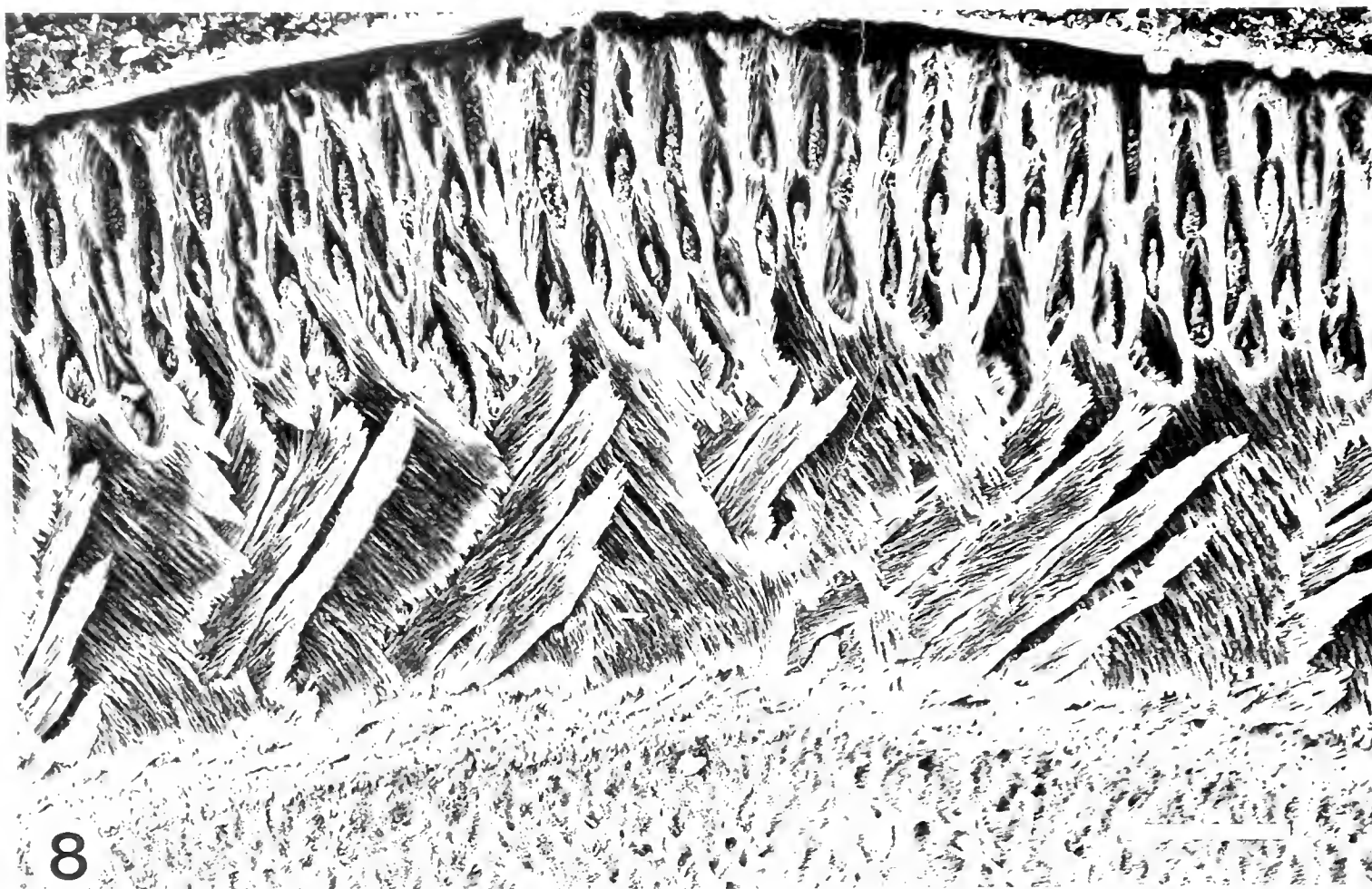
Fig. 8, 9.—8. *Decipomys mongoliensis*, n. gen. and sp., PSS 20 207. SEM micrograph of cross section of lower incisor enamel. EDJ is down and outer surface of enamel is up. In cross section, the absence of prism decussation is clearly evident. In the PI, crystallites within the IPM plates run perpendicular to prism direction. Prisms do not run directly from the EDJ to the outer surface, but are deviated about 45° to the right. In the PE, apically inclined prisms are cut transversely, with IPM shown anastomosing between prisms. Scale bar = 10 μm. 9. *Anomalurus* sp. (MA 85). SEM micrograph of cross section of lower incisor enamel. EDJ is down and outer surface of enamel is up. The cross section clearly reveals the uniserial decussating prism layers in the PI. IPM runs parallel to the prisms and is therefore scarcely visible. In the PE, laterally compressed prisms are cut transversely and IPM anastomoses between them. Scale bar = 10 μm.
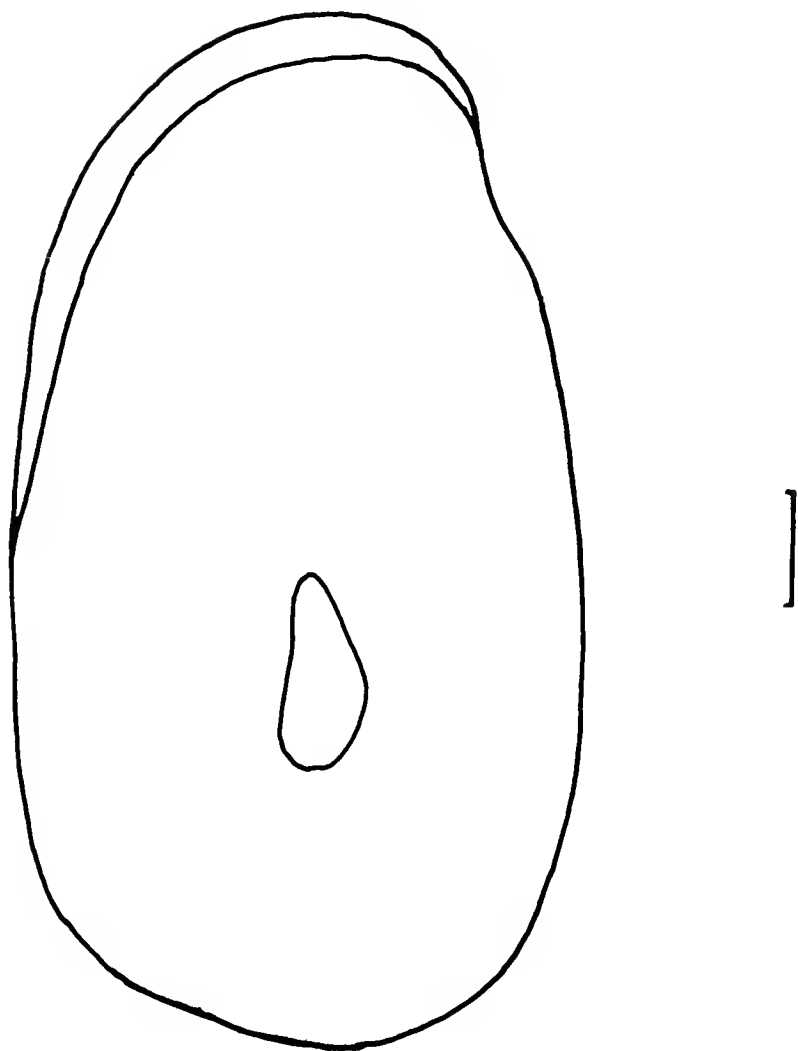
Fig. 10.—Cross section of right lower incisor of *Decipomys mongoliensis*, n. gen. and sp., PSS 20 201. Note the extreme thinness and the asymmetrical distribution of enamel, which extends far on the lateral side. Scale bar = 100 μm.

crown pattern, molar wear facets, and inferred mode of chewing found in advanced mixodonts is not observed in primitive forms (*Zagmys*, *Khaichina*, *Eomylus*).

The upper teeth of *Decipomys* remain unknown, so it is impossible to investigate directly the occlusion between lower and upper cheek teeth. The upper dental formula is probably reduced with only P^4–M^3. The crown pattern of these upper teeth is probably characterized by a large paracone and reduced metacone, and a weak or absent hypocone. These upper molars must also be narrow. Regarding their wear facets, it can be deduced from the lower cheek teeth that wear facet 2 is preeminent (= facet 1 in Crompton, 1971).

Summary.—*Decipomys mongoliensis* shows a unique combination of primitive and derived character states that in our opinion warrant recognition at the familial level. Primitive characters known for *Decipomys* include a sciurognathous dentary bearing a short diastema and large symphysis, and cheek teeth with trigonids higher than talonids, prominent metaconids, closed trigonid basins, and the possible retention of a vestigial paraconid on M_1. Derived characters known for *Decipomys* include a dentary bearing a single, enlarged mental foramen, a pronounced ventral masseteric crest, and an inclined (rather than vertical) ascending ramus; a chin process; probable anisognathy; a lower incisor that extends posteriorly beyond M_3 and which possesses tangential enamel in its portio interna; reduced lower dental formula of 1–0–1–3; and cheek teeth bearing strong wear facets 2–3b, a stair-like profile in lateral view (implying ectental chewing), cusps that are canted anteriorly, a reduced talonid, a sinusid that communicates with the mesoflexid (cristid obliqua absent), a strong hypolophid, subisodonty, and bilateral subhypsodonty.

Discussion and Comparisons.—In their review of rodent and lagomorph origins, Li et al. (1987) consider the cohort Glires to comprise two superorders: Duplicidentata, including orders Mimotonida ("MgMidae" and Mimotonidae) and Lagomorpha; and Simplicidentata, including orders Mixodontia (Rhombomylidae and Eurymylidae) and Rodentia. Here, we adopt this systematic
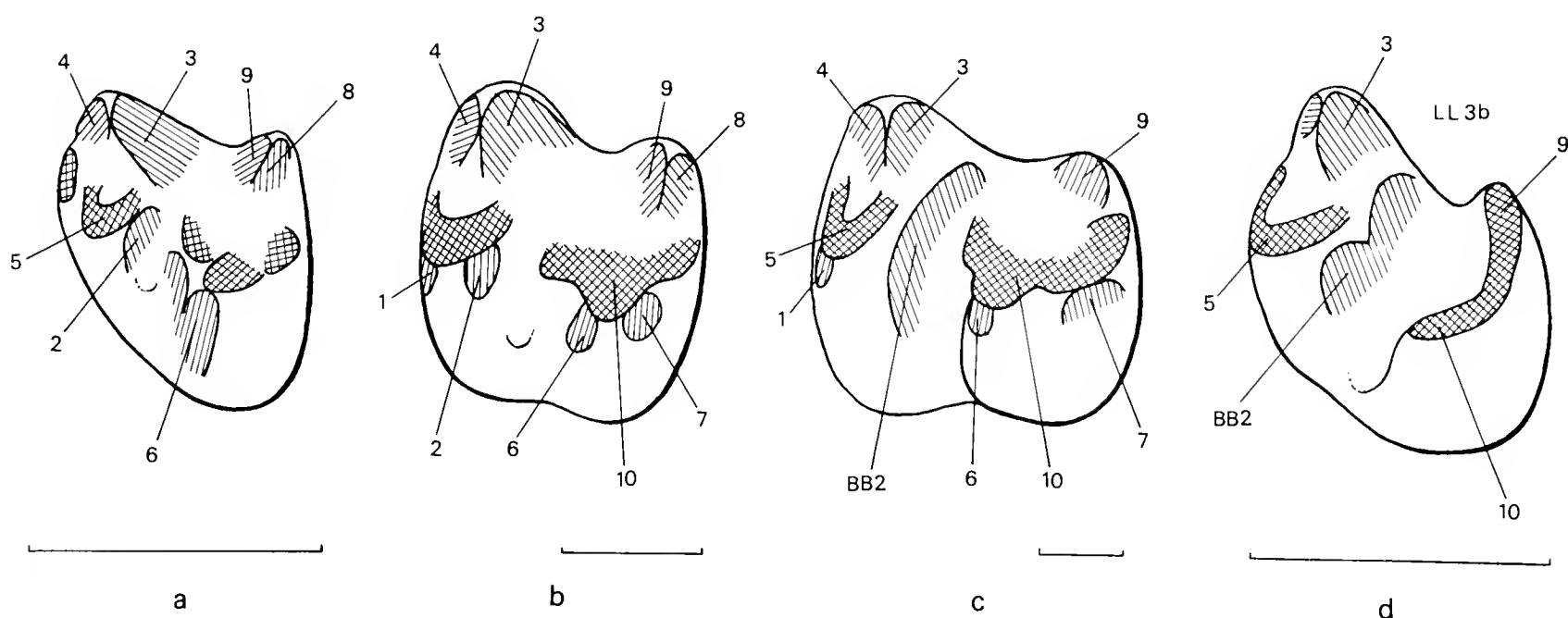

Fig. 11.—Semibuccal view of lower molars (M_2) of Glires known from Tsagan Khushu, Quarry 1. a. *Alagomys inopinatus*, PSS 20 177. b. *Sharomys singularis*, PSS 20 02. c. *Rhombomylus* sp., cf. *R. turpanensis*, PSS 20 165. d. *Decipomys mongoliensis*, n. gen. and sp., PSS 20 208. Nomenclature of wear facets follows Butler (1980). Facets 1, 2, 6, and 7 are buccal (BB) facets that correspond to contact between buccal cusps. Facets 3 and 9 are lingual (LL) facets, corresponding to contact between lingual and buccal cusps. Facets 5 and 10 are lingual–buccal (LB) facets, made during lingual phase and resulting from contact between lingual and buccal facets. In *Decipomys mongoliensis* and *Rhombomylus* cf. *turpanensis* the well-developed BB2 facets indicate important transverse movement. Subhorizontal wear = crossed and main slope = hatched. Scale bar = 1 mm.

Table 3.—*Character analysis of selected dental and anatomical features of lower jaw in early Glires. Taxa examined include* Eomylus, Eurymylus, Mimotona, Gomphos, Khaichina, Rhombomylus, Amar, Zagmys, Cocomys, Heonys, Tamquammys, Paramys, Anagalomys, Ivanantonia, Lushilagus, Decipomys, *and* Barunlestes. *Primitive character states are coded as "0," derived states are coded as positive integers.*

Dentary

1. Horizontal ramus elongated (0); shortened (1).
2. Diastema absent or very short (0); important (1); important and concave (2).
3. Symphysis large and elongated (0); reduced (1).
4. Masseteric fossa posterior (0); below M_3 (1); below M_2 (2).
5. Root of vertical ramus posterior (0); near M_3 (1).
6. Dual mental foramina (0); single mental foramen (1); single, enlarged mental foramen (2).
7. Masseteric crest weak (0); strong (1).
8. Canine present (0); absent (1).
9. I_1 present (0); absent (1).
10. I_3 present (0); absent (1).
11. dI_2 not enlarged (0); enlarged (1).
12. dI_2 surrounded by enamel (0); enamel restricted to buccal side (1).
13. dI_2 with double-layered enamel (0); single layer of radial enamel (1); PE with radial enamel reduced (2).
14. Lower incisor extends posteriorly below M_2 (0); extends below M_3 or farther (1).
15. Radial enamel (0); Hunter-Schreger bands (1); tangential enamel present in PI (2).

Premolars and Molars

16. P_2 present (0); absent (1).
17. P_3 present (0); absent (1).
18. P_4 present, simple cusp (0); P_4 molarized (1); P_4 absent (2).
19. M_1 paraconid present (0); absent (1).
20. Mesoconid absent (0); present (1); present and crestiform (2).
21. Talonid wider than trigonid (0); subequal to trigonid (1).
22. Cheek teeth brachydont (0); unilaterally subhypsodont (1); bilaterally subhypsodont (2).
23. Metaconid prominent (0); metaconid = protoconid (1).
24. Trigonid taller than talonid (0); trigonid and talonid similar in height (1).
25. $P_4 < M_1 < M_2 < M_3$ (0); cheek teeth subisodont (1).
26. M_3 elongated (0); not elongated (1).
27. Hypoconulids absent on M_{1-2} (0); present, moderate in size (1); present, enlarged (2).
28. Talonids of M_{1-2} not compressed anteroposteriorly (0); compressed anteroposteriorly (1).
29. Talonid basin closed (0); sinusid and synclinid communicate (1).
30. Wear facet 10 oblique (0); horizontal (1); wear facet BB2 and LL3b developed (2).

viewpoint and tentatively propose to include the new family Decipomyidae in the order Mixodontia.

In order to compare *Decipomys* with other contemporaneous genera of Glires, we have undertaken a PAUP analysis using characters available on mandibles and teeth of representative genera of Mixodontia, Mimotonida, Rodentia, and Lagomorpha. These characters are listed in Table 3, and Figure 12 shows the character states observed in different genera and the majority rule consensus tree that resulted from our PAUP analysis. From the distribution of alternative character states it appears that: characters 1–7 are generally primitive in Mixodontia and Mimotonida, but derived in Rodentia; characters 21–29 are frequently primitive in Rodentia but derived in Mixodontia; the most derived taxa are *Ivanantonia* (24 derived characters) and *Paramys* (21) for Rodentia and *Decipomys* (23) for Mixodontia; and hypsodonty occurs in early Mixodontia, Mimotonida, and Lagomorpha but not in contemporaneous rodents. In terms of incisor enamel ultrastructure (character 15), it appears to be significant that all rodents and mixodonts for which conditions are known, with the notable exception of *Decipomys*, have HSB in the portio interna. *Decipomys* has tangential enamel in its portio interna, which is also a derived condition, but one that is fundamentally different from HSB.

Decipomys appears to be the sister group of middle Eocene *Lushilagus*, the oldest recognized lagomorph, within a broader assemblage that includes advanced Mixodontia, Mimonotonida, and Rodentia. Provisionally, we propose to include the new family Decipomyidae in the order Mixodontia, but we emphasize that this decision is based only on knowledge of the lower jaw and teeth.

The bilophodont crown pattern of *Decipomys* is unknown in other mixodonts, all of which are larger than *Decipomys* and none of which show similar reduction of the talonids of the cheek teeth. The oldest known lagomorphs, *Lushilagus* and *Shamolagus*, have a bilophate crown pattern, but the hypsodont teeth of these animals render their precise crown pattern unobservable, so meaningful comparisons with *Decipomys* are impossible. Moreover, we note three important differences between *Decipomys* and *Shamolagus*: 1) the shape of the lower jaw of *Shamolagus* is very rabbit-like (see Li, 1965), and therefore different from that of *Decipomys*; 2) there are two mental foramina in *Shamolagus*, but only one occurs in *Decipomys*; 3) P_3 is present in *Shamolagus* (as in all lagomorphs), but this tooth is absent in *Decipomys*.

Incisor enamel ultrastructure remains unknown in *Lushilagus* and *Shamolagus*. Single-layered enamel with HSB is known to be present in the incisors of some leporids, but Koenigswald (1995) has observed two-layered or multilayered incisor enamel in ochotonids, which appears to be the primitive condition for lagomorphs. However, no lagomorph has been reported to possess the combination of inner tangential enamel and outer radial enamel that occurs in *Decipomys*.

Several derived rodent clades show crown patterns very similar to that of *Decipomys*, and these are reviewed here.

The semifossorial African family Pedetidae has an obscure

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Fig. 12.—Character-state distribution of selected dental and anatomical features of the lower jaw in early Glires, mapped onto a strict consensus of 103 trees (Rohlf's C.I.= 0.535). See Table 3 for description of primitive and derived character states. Open rectangles are primitive, black rectangles are derived, black diamonds are more advanced (except in the case of character 15, where the black diamond corresponds to an alternative apomorphy).
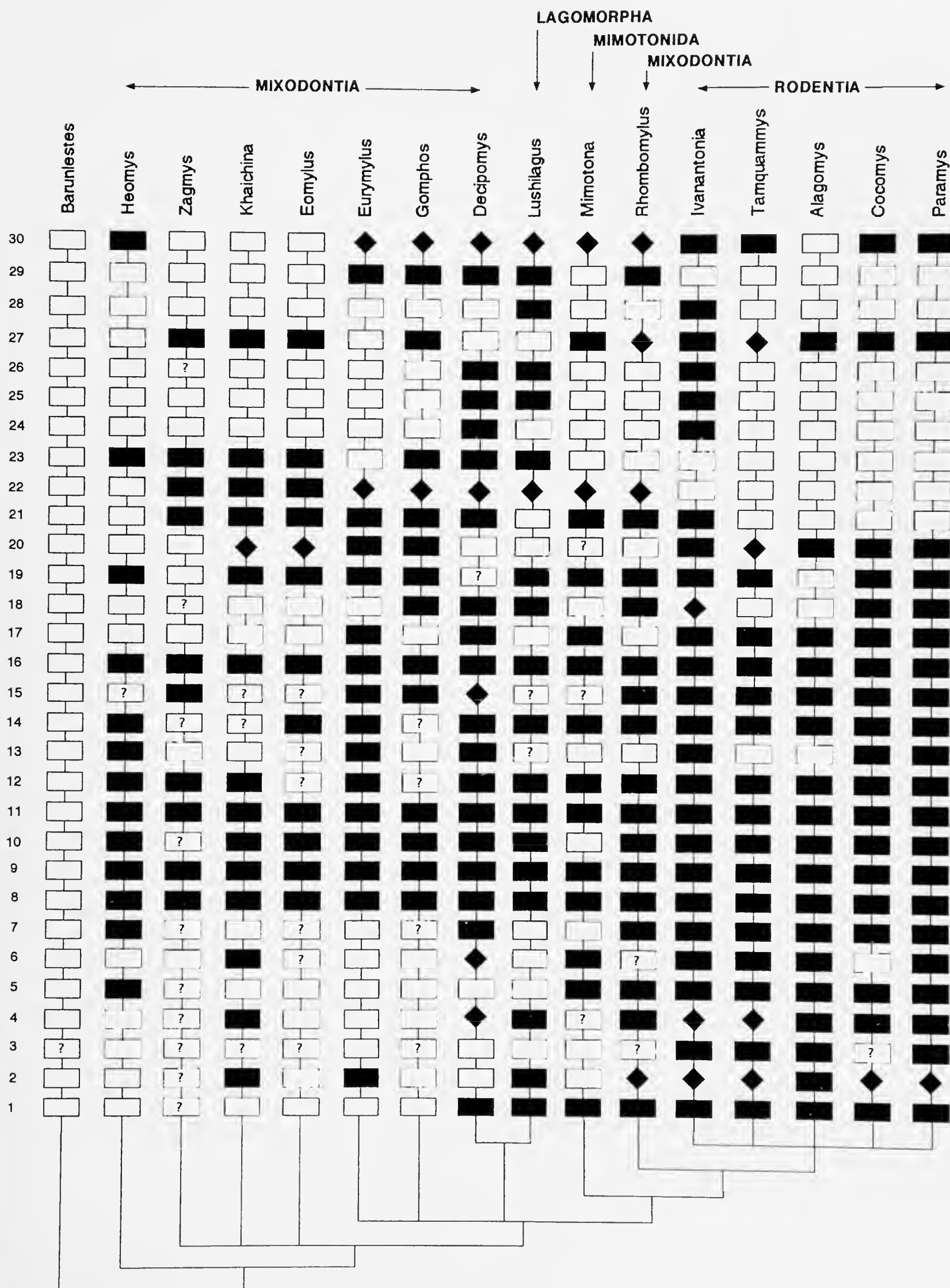
origin, and the question of its phylogenetic position with respect to other families of rodents is still a challenge. Its earliest fossil record occurs in the Lower Miocene of Africa, so the temporal gap between early Eocene *Decipomys* and early Miocene *Parapedetes* and *Megapedetes* may argue against a close evolutionary relationship between the two families. Pedetidae have hypsodont cheek teeth, the occlusal surfaces of which are flattened. Concerning mastication, it has been observed in extant *Pedetes capensis* that chewing movements are bilateral and propalinal (Offermans and de Vree, 1990), which is totally different from the mode of mastication that is inferred to have occurred in *Decipomys*. Additionally, *Pedetes* has derived multiserial HSB with rectangular plate-like IPM in the incisors, which is a basic difference from the tangential enamel of *Decipomys* (Martin, 1995). Considering these points, a close evolutionary relationship between these two families cannot be suggested.

The possible geomyoid rodent *Griphomys* also shows similarities to *Decipomys* that merit discussion here. For example, in both forms the size and position of the mental foramen are similar, and Wilson (1940) noted that the lower jaw of *Griphomys* is robust, as is the case for the new genus. On the other hand, one of the main differences between *Decipomys* and *Griphomys* concerns the size and shape of the diastema of the dentary, which is very short and nearly straight in *Decipomys*, but long and concave (i.e., more typically rodent-like) in *Griphomys*. Concerning the cheek teeth, the most striking similarity is the bilophate crown pattern that occurs in both forms. Nevertheless, some important differences exist: 1) the bilophate condition is less advanced in *Decipomys*, in which the components of the trigonid (protoconid, metaconid, metalophid II) remain clearly visible; 2) the trigonid is notably higher than the talonid in the cheek teeth of *Decipomys*, which is definitively not the case in *Griphomys*; 3) with regard to jaw movement and wear facets, *Griphomys* appears to differ fundamentally from *Decipomys* and all mixodonts in lacking a wear facet along the posterior wall of the anterior crest (BB2–LL3b; see Lillegraven, 1977), which excludes a preeminent ectental movement during mastication in *Griphomys*; 4) the two lophids in *Griphomys* are concave anteriorly, which is not the case in *Decipomys*; 5) a minute mesoconid and an ectostylid occur in *Griphomys*, but are absent in *Decipomys*; 6) in *Griphomys* P$_4$ appears to be reduced and triangular, which is a notable difference from the new genus. In light of these comparisons it seems clear that similarities in tooth pattern observed in *Griphomys* on the one hand and *Decipomys* on the other are superficial, so that a close phylogenetic relationship between the two forms cannot be inferred.

As a matter of interest, we cite another bilophate rodent from the European fossil record: the Oligo–Miocene eomyid *Ritteneria*. However, this semihypsodont genus shows a flattened occlusal surface of the teeth that contrasts markedly with the crown pattern in *Decipomys*, rendering any hypothesis of close phylogenetic relationship between these forms unwarranted.

Among theridomyoids, *Remys* and *Pairomys* show similarities to *Decipomys* that merit consideration. Both theridomyoid genera are minute rodents found in late Eocene rocks of southern France and Spain (Thaler, 1966; Hartenberger, 1973, 1988; Vianey-Liaud et al., 1994). *Remys* and *Pairomys* show slight morphological differences in the talonid: the ectolophid is generally complete in *Remys*, but interrupted on the lingual side in *Pairomys*. Both *Remys* and *Pairomys* have been included in the subfamily Remyinae, which has been attributed to the Theridomyoidea. However, to date, only a few jaws and teeth are available for these taxa. Cranial evidence to confirm this attribution is largely lacking; only a fragmentary maxilla shows that the infraorbital foramen is large as it is in primitive theridomyids, but this character also occurs in other rodents, such as the primitive ctenodactyloid *Tamquammys*.

Before comparing *Remys* and *Pairomys* with *Decipomys*, the rodent characters of Remyinae must be noted: the diastema of *Remys* (Hartenberger, 1988:fig. 2–4) has a rodent-like shape and in lateral view the tooth row appears flat rather than stair-like. The lower cheek-tooth pattern in both *Remys* and *Pairomys* is simplified like that of *Decipomys*, and the trigonids of the cheek teeth in all three genera offer the same design. In fact, the main difference lies in the structure of the talonids of the cheek teeth: in *Decipomys* the posterolophid is emphasized and the ectolophid is suppressed, whereas in Remyinae the ectolophid *and* the posterolophid are always present. In *Pairomys* the ectolophid is interrupted, but the buccal part remains clearly visible. Because of these differences, it appears that the similarites in tooth pattern between *Decipomys* and Remyinae are superficial.

The genus *Fallomus*, known from the Miocene of Pakistan, was described as Chapattimyidae incertae sedis by Flynn et al. (1986). The lower cheek teeth are bilophodont with inclined cusps, and the anterior cusps are very similar to those of *Decipomys*. However, in *Fallomus* an ectostylid is always present in the valley between the protoconid and talonid, and a distinct hypoconulid is also manifest. These are important differences from *Decipomys*. Nevertheless, Flynn et al. (1986:17–18) noted an important inclined transverse wear surface in *Fallomus* and suggested that "Chewing in this taxon was unlike that of other chapattimyids. . . ." Our knowledge of *Fallomus* is still limited to a few isolated teeth. Therefore, we must keep in mind that *Fallomus* shares some interesting similarities in crown pattern with *Decipomys*. Nevertheless, as far as the group is currently known, chappatimyids differ from *Decipomys* in having either pauciserial enamel (Eocene forms) or multiserial HSB in the incisors (Martin, 1993, 1995).

The schmelzmuster present in the incisors of *Decipomys* differs clearly from that of rodent and mixodont incisors. All rodent incisors investigated so far, even those of the oldest known rodents such as late Paleocene cf. *Acritoparamys atavus* from Montana (Martin, 1992), early Eocene paramyids from Silveirhina, Portugal (Flynn et al., 1987), early Eocene *Cocomys lingchaensis* from Hendong County, China, and other early ctenodactyloids have well-developed HSB in the PI (Martin, 1993). HSB likewise characterize all mixodonts investigated so far (*Zagmys*, *Gomphos*, and *Rhombomylus* with one-layered enamel; and *Eurymylus* with two-layered enamel [Flynn et al., 1987; Martin, 1992, 1993]). HSB are formed by decussating layers of prisms and are easily recognized in longitudinal and cross sections. Within the HSB, all prisms run parallel to one another, but in adjacent bands they decussate at a high angle. This regular decussation of prism layers occurs in no other enamel type and is interpreted as a strengthening device that protects against crack propagation (the "plywood effect"; Pfretzschner, 1988).

The incisor enamel of *Decipomys mongoliensis* lacks any decussation of prisms, because prisms run parallel in the PI and PE. The simultaneous turn of prisms in an apical direction at the boundary between PI and PE does not change their orientation with respect to one another. The simultaneous turn of prisms is most likely an adaptation to strengthen the enamel and to prevent crack propagation (Koenigswald, 1988). In particular, tangential enamel with thick IPM plates and crystallite orientation at 90° to prism direction provides a biomechanically similarly effective structure as uniserial HSB. Besides HSB, tangential enamel with

IPM plates is another means of creating the "plywood effect" and is considered to be a derived structure by biomechanical constraints. Derived tangential enamel cannot be a structural predecessor of HSB, because HSB originate from primitive radial enamel with parallel IPM (Koenigswald et al., 1987) and likewise have parallel IPM in the beginning (Martin, 1992). Any angular intersection of prisms and IPM is a derived condition.

Koenigswald (1980) first described tangential enamel in molars of *Mimomys* (Arvicolidae), in which it always occurs with HSB in the same tooth, however. Tangential enamel has also been observed in the incisors of soricids (Koenigswald, 1988), the multituberculates *Mesodma* (Sahni, 1979) and *Ptilodus* (Carlson and Krause, 1985), the extant marsupials *Macropus rufus* and *M. giganteus* (Koenigswald, 1994), and the extinct marsupial *Groeboria minoprioi* (Koenigswald and Pascual, 1990). Recently, Koenigswald (1995) observed tangential enamel in the upper incisors of the Pleistocene ochotonid *Prolagus sardus*; in the lower incisors, however, HSB are present in addition to radial enamel.

The earliest occurence of this enamel type is, according to Carlson and Krause (1985), in the Lancian (late Cretaceous), while the oldest HSB date back only to the early Paleocene (Koenigswald et al., 1987).

Radial enamel with parallel IPM is the primitive condition for placentals and marsupials and has been observed in molars of the early Paleocene condylarth *Conacodon*, for example. The earliest record of HSB so far is in an early Paleocene arctocyonid from the San Juan Basin (New Mexico), in which they form a central zone of decussating prisms in the radial enamel of the molars. This indicates that HSB evolved directly from the radial condition. In the late Paleocene *Arctocyon matthesi* from Walbeck, Germany, the entire enamel is formed by distinct HSB (Koenigswald et al., 1987).

Because all rodent and mixodont incisors investigated so far have clearly developed HSB (Korvenkontio, 1934; Walhert, 1968; Sahni, 1980; Flynn et al., 1987; Martin, 1992, 1993, 1995) which can easily be derived structurally from the most ancient mammalian HSB, *Decipomys* most likely can be excluded from Rodentia. At least two rodent taxa with pauciserial HSB, *Ivanantonia efremovi* and *Alagomys inopinatus*, are associated with *Decipomys* in the Tsagan Khushu fauna.

CENOGRAM ANALYSIS OF THE TSAGAN KHUSHU MAMMALIAN FAUNA

In order to understand the early history of Glires and to place it in its paleoecological context, an analysis of the Tsagan Khushu mammalian fauna has been undertaken using the cenogram method (Legendre, 1986, 1989). Quarry 1 and Quarry 2 were analyzed together in order to document the entire range of mammalian body sizes (i.e. small and large species), and because of the very short time interval between the two quarries assumed by Russell and Zhai (1987).

A cenogram is a graph proposed by Valverde (1964, 1967) showing the body-size distribution of species within a mammalian community. It is built by plotting the mean body weight of each species on the Y axis, ranked in decreasing-size order on the X axis. The mean body weight of the Tsagan Khushu species was estimated from M_1 area (i.e., length $\times$ width) using regression parameters taken from Legendre (1989:table 1). For extinct orders, the parameters used were those calculated for all herbivores.

The cenogram obtained for Tsagan Khushu (Fig. 13a) shows that the range in mean body weights of species covers that observed in extant faunas, that is, from about 2 g for the smallest species (*Tsagan-*

ius ambiguus) to about 600 kg for the largest (*Coryphodon tsaganensis*). The pattern of distribution of body sizes of species within extant faunas is related to their environment (Legendre 1986, 1989; Legendre et al., in press). No large gap appears in the body-size distribution of the Tsagan Khushu fauna, but a small offset is present at about 1 kg. Medium-sized and large-sized species (above 500 g) are less abundant than small-sized species (less than 500 g). Thus, the environment of the Tsagan Khushu fauna was not very humid and rather forested. Similar patterns in extant mammalian faunas are found in western Durango or Colima (western coast of northern Mexico), which roughly correspond to seasonal forest environments (Legendre et al., in press). Nevertheless, due to possible sampling bias, this example must be considered cautiously.

The distribution of rodent species (Fig. 13b) approaches that of extant rodents within the small-sized category as early as the early Eocene. The Mixodontia are generally larger than the rodents except for the minute *Decipomys mongoliensis*. Compared with the distribution of modern rodent families, the mixodonts occupy the sciurid range, while the Tsagan Khushu rodents occupy the size range of murids.

CONCLUSIONS

SYSTEMATIC POSITION OF DECIPOMYIDAE

We can conclude from this study that among all other Glires, Decipomyidae occupy a peculiar po-

sition. This new family cannot be considered as Rodentia: incisor enamel, the short diastema, and jaw movement as inferred from molar wear facets are
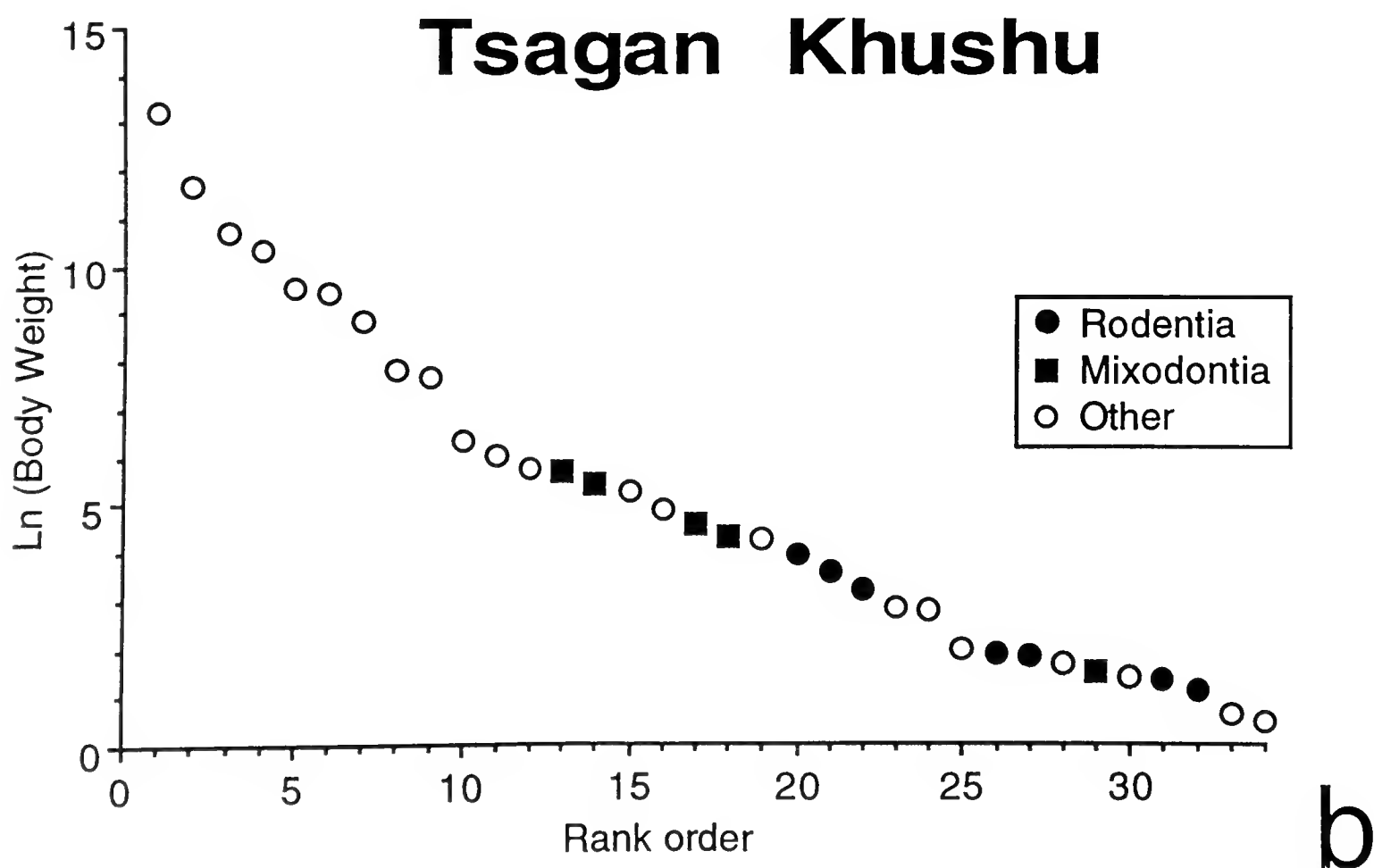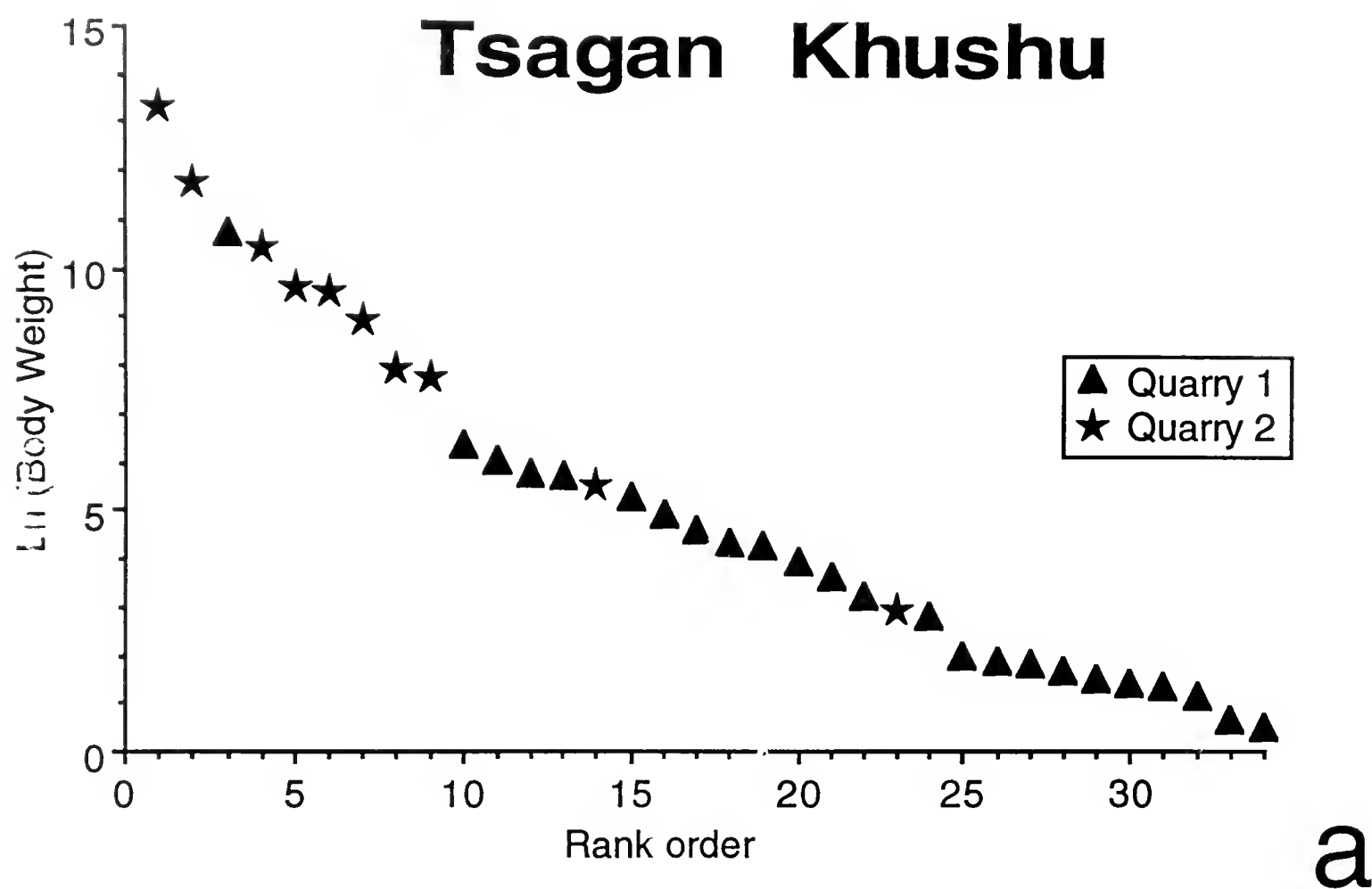
Fig. 13.—Cenogram for the Tsagan Khushu mammalian fauna. a. Mammals of Quarry 1 (triangles) and Quarry 2 (stars). b. Size range of rodents (filled circles) and mixodonts (filled squares).

all characters that have not been observed in rodents. We also note important differences from Lagomorpha (shape of the jaw, P_3 absent, single mental foramen) that do not allow us to assign Decipomyidae to Lagomorpha, even if *Decipomys* appears to be more closely related to Lagomorpha than to any other Glires. As such, we prefer to consider it as an advanced mixodont representing a new family. However, *Decipomys mongoliensis* is very different from all other known mixodonts: its incisor enamel, small size, loss of P_3, isodont tooth row (and short M_3), and unique mental foramen, distinguish *Decipomys* from other mixodonts. It also appears that this form has no known descendant. Once this form becomes better known, it may even become desirable to recognize *Decipomys* as pertaining to a new order, but without adequate material (upper teeth and skull) this action cannot be sustained at this time.

EARLY HISTORY OF GLIRES

Recent discoveries in Asia have shown that this area is the probable center of origin and subsequent dispersal of Glires: in the late Paleocene and early Eocene of Asia, four orders (Mixodontia, Mimotonida, Lagomorpha, Rodentia) including at least ten families have been recognized to date. In the Paleocene of China and Mongolia, the Eurymylidae are abundant and diverse and can be considered as the stem group for this cohort. However, this paleontological evidence does not explain the very different histories of the two extant orders, Rodentia and Lagomorpha: in the Recent fauna we can recognize 1752 species of rodents comprising about 30 families but only 65 species of lagomorphs comprising two families. It has been argued frequently that the early adaptation to herbivory in lagomorphs could be the main obstacle for future diversification. It seems that study of the Tsagan Khushu fauna and its ecological and geological context could contribute to a better understanding of the early history of Glires, and thus give some explanations for the differences in diversity characterizing modern rodents and lagomorphs.

Russell (1975) has demonstrated with paleontological data that in continental Europe the early Eocene climate was warmer than in the Paleocene, becoming more or less tropical, and in this area these conditions persist into the middle Eocene. Indeed, this warming trend appears to have been global: near the Paleocene–Eocene transition, a major temperature fluctuation is observed in the marine realm and this event can be correlated with continental carbon isotope fluctuations in the early Eocene of North America (Rea et al. 1990; Koch et al., 1992). Because in North America (and Europe) this interval marks important evolutionary changes in mammalian faunas, Koch et al. (1992:322) proposed that "the marine and continental linkage provided by carbon isotopes indicates a more prominent role for climate warming in the evolution of Paleogene land mammals than previously realized."

Our cenogram analysis of Tsagan Khushu suggests that early Eocene Asian Glires radiated into the general body-size niches of the Recent forms within a not very humid woodland habitat. Nevertheless, we note that rodents and mixodonts differ significantly in size range: rodents are generally smaller than contemporary mixodonts, occupying similar size niches as extant murids. The age of this local fauna is more or less contemporaneous with the Paleocene–Eocene transition, and therefore near the beginning of the warming interval previously discussed. In the middle Eocene almost all mixodonts are extinct, and until the middle Eocene lagomorphs are unknown on other continents: their first record outside of Asia is in the middle Eocene of North America; they appeared subsequently in the early Oligocene of Europe and the Miocene of Africa. On the other hand, the early history of rodents is totally different: from the late Paleocene–early Eocene rodents are known from North America and Europe (and were probably present in North Africa), and so from this early date rodents were able to disperse over all Holarctic continents and to diversify. Therefore, climatic warming favored the dispersal of rodents and not mixodonts. We have noted that in Asia the oldest rodents are small animals with brachydont teeth, but mixodonts, with the exception of *Decipomys*, are larger animals with semihypsodont molars. This larger size could be another reason for the reduced evolutionary success of mixodonts. The first "large" rodents (*Marmota*-sized) are known from the late early Eocene in North America and Europe. Therefore, we suggest that the post-Tsagan Khushu interval is a critical turning point in the history of Glires, and that the evolutionary success of Rodentia is established by this time. The climatic warming of the Paleocene–Eocene transition probably plays an important role for the differential evolutionary success observed in Rodentia and Lagomorpha.

ACKNOWLEDGMENTS

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A REPORT ON THE EOCENE ANDARAK MAMMAL FAUNA OF KYRGYZSTAN

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ABSTRACT

A vertebrate-bearing locality at Andarak 2 in Kyrgyzstan has yielded a diverse mammalian fauna that includes Proteutheria and/or Lipotyphla, Micropternodontidae, Mixodontia, Lagomorpha, Rodentia, Mesonychia, Creodonta, Perissodactyla, Artiodactyla, and possibly Proboscidea. Biostratigraphic analysis of the mammalian fauna suggests a late Ypresian–early Lutetian age for the locality, whereas the elasmobranchian fauna, microfossils, and stratigraphy favor a late Ypresian age (latest early Eocene). The mammal assemblage is most similar to those from Khaychin Ula in Mongolia (early Lutetian).

INTRODUCTION

During the last decades, our knowledge of the Paleogene mammals of Asia has increased greatly, mainly through discoveries in China, Pakistan, India, and Kazakstan. Most Asian Paleogene localities occur in continental sequences that cannot be directly correlated with marine strata. Because of the high degree of endemism characteristic of many Asian Paleogene mammal faunas, correlation between Asian Paleogene faunas and European or North American mammalian biochronologies is often difficult (e.g., Savage and Russell, 1983; Russell and Zhai, 1987; Holroyd and Ciochon, 1994; Meng et al., 1998; Ting, 1998; Wang et al., 1998). In this context the Andarak mammal fauna from Kyrgyzstan is important—its mammals were deposited in a marine bed in association with abundant remains of invertebrates and fishes.

There are two mammal-bearing sites, Andarak 1 and 2, in the vicinity of Andarak village near Isfana, in the Lyajlak District of Osh Province, Kyrgyzstan. Andarak 2, the more productive of the two sites, was discovered in 1968 by A. K. Rozhdestvenski (for more details, see Russell and Zhai, 1987). Since 1988 the first author has undertaken further field work and study of Andarak 2 mammals, and both of us have collaborated on this project since 1995. Here, we provide a summary of our current knowledge of the Andarak mammals and their age and paleobiogeographic affinities.

Institutional abbreviation used in text: ZIN, Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia.

AGE OF THE ANDARAK 2 LOCALITY

STRATIGRAPHIC POSITION OF THE LOCALITY

The mammal-bearing bed is a layer of weakly indurated marine sand with gravels, which can be screen-washed to yield numerous remains of sharks and rays and a smaller number of fragmentary mammals. This fossiliferous unit is part of an approximately two-meter-thick bed of variably indurated marine sand (for a stratigraphic section of the locality see Gekker et al., 1962; Averianov and Udovichenko, 1993; Averianov, 1994b). The bed is part of the lower Alay beds, which are defined by the first appearance of the oyster *Ostrea turkestanensis* Romanovsky, 1879 (Gekker et al., 1962). Vertebrate remains, mostly shark teeth and turtle shells, can also be found in the overlying limestones of the upper Alay beds. We use the term Alay beds for the "Alay Yarus," a stratigraphic unit that was described as a stage (Gekker et al., 1962).

In earlier geological literature, both the lower and upper Alay beds were considered to be middle Eocene in age, the boundary between the underlying Suzak beds and the Alay beds having been correlated with the lower–middle Eocene boundary. This yielded a middle Eocene age for the Andarak 2 mammal locality (Reshetov et al., 1978; Russell and Zhai, 1987). However, the molluscan fauna of the Fergana Paleogene, on which the regional stratigraphy is largely based, is highly endemic and does not allow direct correlation with western Europe. Recently, the Suzak beds of the southern Fergana region were determined to be late Paleocene in age based on foraminifera (Sultanov and Tsatsyr, 1990). In neighboring Tajikistan, the uppermost Alay beds are correlated on the basis of their nannoplankton fauna with the *Discoaster sublodoensis* zone (NP 14), which is dated as lower Lutetian or latest Ypresian (Musylev and Salibayev, 1988; Berggren et al., 1995). Consequently, with the exception of the uppermost beds, most of the Alay beds (including the mammal-bearing levels) must be lower Eocene, Ypresian equivalent.

Analysis of the Elasmobranchian Fauna

About 40 shark species are known from Andarak 2 (Averianov and Udovichenko, 1993). Among these are three species of stratigraphic significance (Udovichenko, personal communication). *Charcharocles subserratus* is restricted in its stratigraphic distribution in western Europe to the Paniselian beds of Belgium (Casier, 1950), which are equivalent to the uppermost part of nannoplankton zone NP 12 (Steurbaut and Nolf, 1986), i.e. Ypresian. The dasyatid batoid genus *Hypolophodon* is unknown in western Europe in deposits younger than Ypresian (Herman, 1986; Cappetta, 1987). A triakid shark identified as *Galeorhinus* aff. *G. microdon* by N. I. Udovichenko appears at the base of the Upper Bukharian beds (early Ypresian) in the Fergana de-

pression. This form was not found above the lower Alay beds by Udovichenko, who sampled approximately 43,000 shark teeth from the base of the upper Alay beds near Vostochnyi in the southern Fergana region. *Galeorhinus microdon* is characteristic of late Paleocene deposits in the Fergana depression and in southern Kazakstan (Udovichenko, 1989). In conclusion, the shark fauna suggests an early Eocene, probably late Ypresian, age for the Andarak 2 locality.

Sequence Stratigraphy

In the regional Fergana Paleogene section, the Andarak locality is situated in the sands and conglomerates of the lower Alay beds, which are at the beginning of a transgressive cycle (Tejas sea-level cycle TA 3.1; see Haq et al., 1987). The limestones of the upper Alay beds and overlying Turkestanian beds were deposited during maximally transgressive conditions of this cycle (Gekker et al., 1962), which can be correlated with the transgressive maximum found in western Europe at the beginning of the Lutetian. Hence, the lower Alay beds can be correlated with formations deposited immediately prior to the Lutetian transgression, such as the lower part of the Kuldana Formation in Pakistan. In the latter rock unit, fluvial red mudstones were deposited just before Tethys sea transgression, which is indicated by the transitional marine deposits of the upper Kuldana Formation and the limestones of the Kohat Formation (see Russell and Zhai, 1987; Thewissen and Hussain, 1998). In western Europe the beginning of this transgressive cycle occurs approximately at the Ypresian–Lutetian boundary, around 50 Ma (Keller, 1983).

The Andarak fauna contains tropical elements, such as tetraodontiform fishes, boid and sea snakes (Palaeopheiidae), and agamid lizards (Averianov and Danilov, 1996). All of these taxa indicate warm climatic conditions, as is typical for this interval.

THE ANDARAK MAMMAL FAUNA

Mammalian taxa currently known from Andarak 1 and 2 are listed in Table 1. Our ongoing study of this fauna shows that previously published lists of the Andarak mammals require some revision. We suspect that Erinaceomorpha indet. and Dichobunidae indet., cited from the Andarak 2 locality by Reshetov et al. (1978) and Russell and Zhai (1987), may instead be referred to a new diacodexeid genus described by Averianov (1996b). One jaw fragment

with a premolar indicates the presence of a small lipotyphlan or proteutherian. A tiny, isolated M_3 may pertain to a small palaeoryctid. In 1994 Shevyreva reported an alleged eurymylid from Andarak 2 (Shevyreva, 1994). Her published descriptions and figures leave little doubt that the taxon in question is actually a mimotonid mixodontian, described by Averianov (1994b). Averianov's taxon was published in the issue of *Acta Palaeontologica Polonica* which

Table 1.—*Mammalian taxa from Andarak 1 and 2, lower Alay beds, Kyrgyzstan. Taxa collected by workers other than the authors are indicated by an asterisk (specimens of which are deposited in the Paleontological Institute, Moscow).*

Order Proteutheria or Lipotyphla
    genus and species indet.

Order indet.
  Family Micropternodontidae
    Sarcodon udovichenkoi Averianov, 1994a

Order Mixodontia
  Family Mimotonidae
    Anatolmylus rozhdestvenskii Averianov, 1994b
    Aktashmys montealbus Averianov, 1994b

Order Lagomorpha
    genus and species indet.
  Family Mytonolagidae
    Valerilagus reshetovi Shevyreva, 1995

Order Rodentia
  Family Chapattimyidae
    Petrokozlovia sp., cf. *P. notos* Shevyreva, 1972
    Saykanomys sp., cf. *S. bohlini* (Dawson, 1964)
    Advenimus sp., cf. *A. burkei* Dawson, 1964
    Khodzhentia vinogradovi Averianov, 1996

  Family Tamquammyidae
    Alaymys ctenodactylus Averianov, 1993
    ?Adolomys sp.

  Ctenodactyloidea indet.

Order Mesonychia
  Mesonychidae indet.

Order Creodonta
  Family Hyaenodontidae (determined by A. Lavrov, Paleontological Institute, Moscow)
    Neoparapterodon n. sp.
    n. gen. and sp.

Order Perissodactyla
  Family Chalicotheriidae or Equidae(?)
    ?Eomoropus sp. or ?cf. *Propachynolophus* sp.

  Family Rhodopagidae
    Rhodopagus minutissimus Reshetov, 1979
    Pataecops (?) *microdon* Reshetov, 1979

  Family Lophialetidae
    Eoletes sp. (*?Schlosseria*)
    ?Lophialetes sp.

  Family Deperetellidae
    Deperetella ferganica Belyayeva, 1962

  Family Hyracodontidae
    Forstercooperia sp.

  Family Amynodontidae
    Andarakodon kirghisiensis (Belyayeva, 1971)

Table 1.—*Continued.*

Order Artiodactyla
  Family Diacodexeidae
    Diacodexis sp.
    Eolantianius russelli Averianov, 1996b

Order Proboscidea(?)
  Family Anthracobunidae
    Pilgrimella sp.

appeared in November, whereas Shevyreva's description of the "eurymylid" was published in the "October" issue of "*Doklady Academii Nauk*," which actually appeared in December. Hence, we consider *Anatolimys rozhdestvenskii* Shevyreva, 1994 as a junior synonym of *Anatolmylus rozhdestvenskii* Averianov, 1994. More recently, Shevyreva (1995) named two new lagomorph genera and species. The holotype and only known specimen of one of these taxa, *Romanolagus hekkeri*, is not a lagomorph M^1, as was thought by Shevyreva, but M^3 of *A. rozhdestvenskii*. Hence, *Romanolagus hekkeri* is also a junior synonym of *Anatolmylus rozhdestvenskii*. The second taxon described by Shevyreva (1995), *Valerilagus reshetovi*, is a true lagomorph.

The most abundant perissodactyl in the Andarak fauna is the very small tapiroid *Rhodopagus minutissimus*. Reshetov (1979) considered the Rhodopaginae as members of the family Lophialetidae. Subsequently, *Rhodopagus* and *Pataecops* were referred to the Hyracodontidae by Lucas and Schoch (1981). Here, we follow Prothero and Schoch's (1989) classification of perissodactyls, wherein Rhodopagidae are accorded familial rank. However, according to Gabunia and Kukhaleishvili (1991), a skull of *Rhodopagus* from the early Eocene Chakpaktas Svita in the Zaysan Basin of Kazakstan confirms the allocation of this genus to the Lophialetidae. Dashzeveg (1991) expressed some doubts regarding the second small tapiroid species from Andarak, *Pataecops microdon*. This question will remain unresolved until a systematic revision of the tapiroids from the Andarak localities is achieved.

Larger tapiroids are also abundant in the Andarak fauna. They are mainly represented by a species of either *Eoletes* or *Schlosseria*, and a few isolated teeth of a larger lophialetid, possibly *Lophialetes*. *Schlosseria* is very similar dentally to *Eoletes* and *Lophialetes*; however, these latter genera differ by cranial features (Emry et al., 1995). A maxillary fragment from Andarak shows some cranial similarities with *Eoletes*: infraorbital foramen placed

relatively low, close to the tooth row; the zygomatic root begins above M², whereas it begins above M¹ in *Schlosseria*. This specimen differs from *E. gracilis* from the Shinzhaly fauna (Kolpak Svita) by its smaller teeth. *Schlosseria* and *Lophialetes* are usually found in the same beds; hence, they are suspected of being females and males of the same species (Qi, 1987). Could this be the case for the larger lophialetid at Andarak, which would then be *Eoletes* males? Pending resolution of this issue based on better material, we still list the larger lophialetid as "?*Lophialetes* sp." in Table 1.

Pilgrimella sp. was cited in the faunal list of Reshetov et al. (1978). If this determination is correct, the family Anthracobunidae is also present in Andarak fauna.

MAMMAL BIOSTRATIGRAPHY

For purposes of intercontinental correlation of Paleogene strata in Asia, mammal taxa known from both Asia and some other continent are of greatest utility; however, these are rare in Asia. Among the diverse perissodactyls, several families (Rhodopagidae, Lophialetidae, Deperetellidae) are endemic to Asia. We find it interesting that the early equid *Propachynolophus* occurs at Lingcha, Limuping Formation, Hunan Province, China (Li et al., 1979). This record suggests correlation of the Limuping Formation with European reference-level MP 10, correlative with the late Ypresian (Godinot, 1987), unless the Chinese material actually represents a primitive chalicothere or tapiroid (Ting, 1995). In the Andarak mammal assemblage, one lower molar (ZIN O.32758) originally attributed to *Eomoropus* sp. (Averianov and Udovichenko, 1993) can now be referred with some confidence to ?*Propachynolophus* sp. If this taxonomic allocation is correct, it provides another argument in favor of a late Ypresian age for the Andarak fauna. The only genus in the Andarak fauna to be found in North America is *Forstercooperia*, which arrived on that continent in the early Uintan (UN1; Stucky, 1992). Another indirect indication is given by the arrival in North America of an amynodontid (a cadurcodontine) in UN2, and of *Metamynodon*, belonging to the same tribe as the Andarak amynodontid (Metamynodontini; Averianov and Potapova, 1996) in the late Uintan (UN3; Stucky, 1992). These taxa are probably of Asian origin, and the first appearance of *Forstercooperia* in North America indicates an age possibly not too distant from Andarak's age (estimation of the lower limit of Uintan is 48 Ma in Stucky [1992], which would be early Lutetian. However, see Note added in proof at end of this paper.).

The evidence from the artiodactyls is not more precise. On the one hand, the presence of *Diacodexis* would support an early Eocene age. However, the attribution of material from Andarak to that genus requires additional evidence. On the other hand, the new genus *Eolantianius* has a relatively large hypocone, as is characteristic in middle Eocene rather than early Eocene artiodactyls in western Europe and North America.

On the whole, this mammalian biostratigraphical evidence is imprecise. It points toward either a late Ypresian or an early Lutetian age for the Andarak mammalian faunas. At present, we prefer a late Ypresian age based on the marine fossils. In the future, further work on the locality should enable us to give more precise correlations based on marine fossils (including microfossils), and to extend and refine correlations with other mammalian faunas in Asia and elsewhere.

PALEOBIOGEOGRAPHIC ANALYSIS OF THE ANDARAK FAUNA

To elucidate paleobiogeographic differences and areas of endemism, we used a parsimony analysis of endemicity (Rosen, 1988; Morrone, 1994). This analysis is based on a matrix showing the distribution of 61 mammalian families in 16 Asian faunas of early–middle Eocene age (see Appendix). We used all faunas containing ten or more families, plus the Limuping fauna which contains nine families. We could not include the Wutu fauna, which contains 21 families, because the complete list is not yet published (Tong and Wang, 1995). Cetaceans were not considered. The geographic distribution of these localities is shown in Figure 1. The family level was chosen because there are not enough orders, and at the genus level the faunas are too different. The data were taken from Russell and Zhai (1987) and the literature published since this monumental synthesis (Kumar and Jolly, 1986; Qi, 1987; Thewissen et al., 1987; Tong and Lei, 1987; Tong, 1988, 1992; Shevyreva, 1989, 1992; Cheng
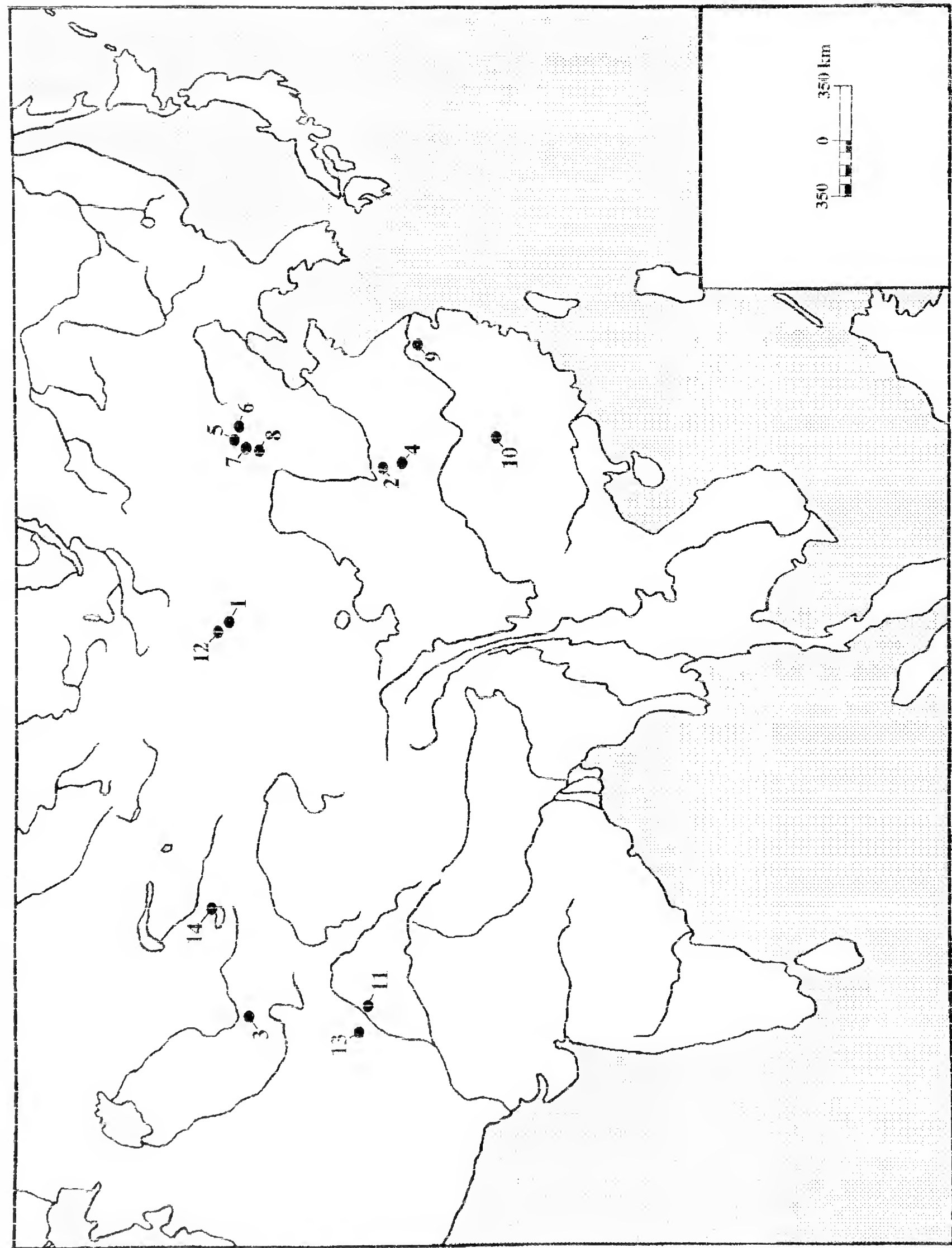
Fig. 1.—Location map of early–middle Eocene localities in Asia. Numbers correspond to the following localities: 1, Tsagan Khushu; 2, Lushi Basin (Upper Lushi Formation) and Yuanqu Basin (Heti Formation); 3, Andarak 2; 4, Xichuan Basin (Yuhuangding and Hetaoyuan formations); 5, Arshanto Formation; 6, Irdin Manha Formation; 7, Camp Margetts area (Irdin Manha Formation); 8, Ulan Shireh Formation; 9, Shanghuang fissure fillings; 10, Hengyang Basin (Limuping Formation); 11, Subathu Formation; 12, Khaychin Ula; 13, Kuldana Formation; 14, Zaysan Basin (Lower Obayla Formation).
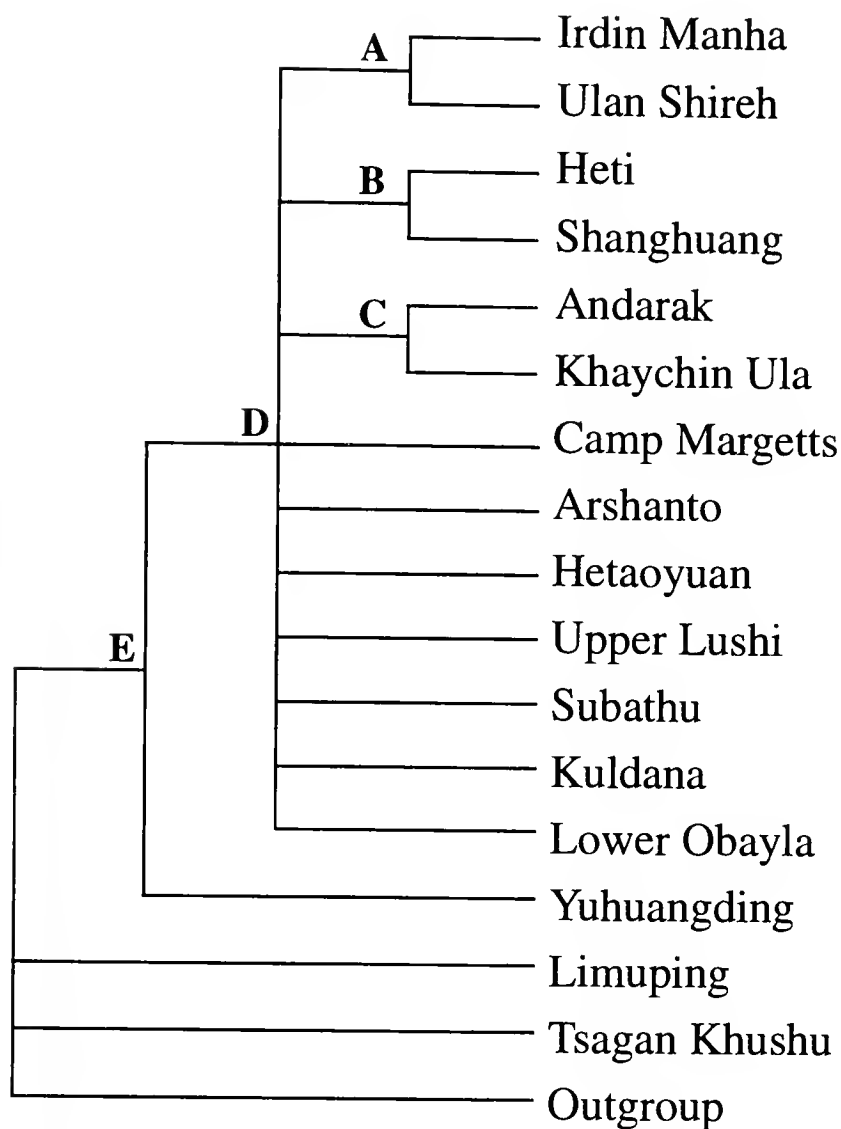
Fig. 2.—Strict consensus tree for data matrix in Appendix. See text for discussion of taxa supporting each node.

and Ma, 1990; Dashzeveg, 1990a, 1990b; Qi et al., 1991, 1996; Ting, 1993, 1995; Averianov, 1994a, 1994b, 1996a, 1996b; Meng et al., 1994; Wang and Dawson, 1994; Beard, 1995; Hartenberger et al., 1995; Hu, 1995; Wang, 1995; Averianov and Potapova, 1996), with a few systematic emendations based on our own observations.

A faunal parsimony analysis using the mhennig* and bb* options in HENNIG 86 produced 12 trees (length, 128 steps; consistency index, 0.47; retention index, 0.46). A hypothetical fauna with 0 for each family was used as an outgroup. In the strict consensus tree (Fig. 2) five groups of localities can be recognized. The first group (node A; Ulan Shireh and Irdin Manha localities) is united by the presence of Hapalodectidae, Didymoconidae, Miacidae, Coryphodontidae, and Helohyidae. The Shanghuang and Heti localities (node B) are united by the presence of Canidae, Tillotheriidae, Tarsiidae, Eosimiidae, Anthracotheriidae, Eomoropidae (or Chalicotheriidae), and Cricetidae. Andarak is united with Khaychin Ula at node C by the presence of Mi-

cropternodontidae, Mytonolagidae, Tamquammyidae ("reversal," this family is not characteristic for the rest of node D), and the absence of Helaletidae (which appeared at node E). Node D includes nodes A–C plus the Lower Obayla, Kuldana, Subathu, Upper Lushi, Hetaoyuan, Arshanto, and Camp Margetts localities. For this group the presence of Mesonychidae, Deperetellidae, Hyracodontidae, Brontotheriidae, and the absence of Eurymylidae and Tamquammyidae is characteristic. The next grouping (node E) unites node D and the Yuhuangding locality. This may be characterized by the appearance of Hyaenodontidae, Lophialetidae, and Helaletidae. The Tsagan Khushu and Limuping (= Hengdong) faunas are closest to the "outgroup" fauna, apparently reflecting the great age of these faunas among those analyzed here. Both are approximately equivalent in age and are correlated with the basal Eocene, early Sparnacian, and early Wasatchian (Ting, 1993). The Yuhuangding fauna is clearly older than faunas united at node D (including the Hetaoyuan fauna which comes from the same area) by the presence of Eurymylidae and Tamquammyidae, and the absence of some families listed above for node D. Within node D only the Shanghuang and Heti faunas are united by the presence of endemic groups. These faunas are given different ages, Irdinmanhan (Lutetian) and Sharamurunian (Bartonian) respectively (Holroyd and Ciochon, 1994). Their close similarity can be explained by ecological factors, both representing forested environments, and by their position in the same zoogeographical province. The abundance and diversity of primates in the Shanghuang and Heti faunas indicates the presence of forested environments in this region. In sharing the presence of "primates" (here including carpolestids) and ischyromyid rodents, the Shanghuang fauna also resembles the much older (basal Ypresian) Wutu fauna, which samples a swampy environment (Tong and Wang, 1995). Except for these assemblages and the Arshanto fauna of Inner Mongolia (Qi, 1987), true ischyromyid rodents in Asia have been found only at the Zhylga locality in southern Kazakstan, the mammalian fauna of which lived near the Tethys coast during the early Ypresian, also under forested and humid conditions (Averianov and Erfurt, 1996). Differences between faunas united at nodes C (Andarak and Khaychin Ula) and A (Ulan Shireh and Irdin Manha) may be explained by biogeographic or ecological factors as well as age differences. The presence and abundance of Mytonolagidae and Tamquammyidae at node C and Coryphodontidae at node A are appar-

ently caused by biogeographic or ecological factors, reflecting more arid environments in the former group and more humid conditions in the latter. In contrast, the presence of Helohyidae at node A probably reflects the younger age of these faunas. The Arshanto fauna is somewhat intermediate in composition between nodes A (Coryphodontidae) and C (Micropternodontidae).

The parsimony analysis shows that the Andarak fauna is most similar to the Khaychin Ula fauna from Mongolia, and lies within a group of mostly middle Eocene faunas.

CONCLUSIONS

Preliminary data from the shark fauna and sequence stratigraphy suggest a late early Eocene (late Ypresian, Cuisian equivalent) age for the Andarak fauna. Some elements of the mammal fauna support this hypothesis, whereas others indicate affinities with middle Eocene (Lutetian) faunas. We consider the late Ypresian age to be the best supported choice at present. This hypothesis should be clarified by future work at this locality. The Andarak mammal fauna is remarkable for its occurrence within a marine series. Publication of the studies of sharks and further analysis of marine microfossils should allow a better supported and more precise correlation of this fauna with marine stages, thus providing an important point of correlation for Asian mammalian faunas. The search for and study of the Andarak mammals will also be continued.

According to our analysis of stratigraphic data, the Andarak fauna is roughly contemporaneous with mammal assemblages from the lower part of the Kuldana Formation in Pakistan, the Middle and Upper Obayla Svita in the Zaysan Basin (not included in our analysis due to incomplete data), the Arshanto Formation in Inner Mongolia, and the Yuhuangding Formation in Henan. If so, differences between these faunas and that known from Andarak must reflect zoogeographical, ecological, or taphonomic factors. Other faunas, including those from the Lower Obayla Svita, the Bumban Member of the Naran Bulak Svita at Tsagan Khushu, the Wutu Formation, and possibly the Limuping Formation, are older. Assemblages from Irdin Manha, the Hetaoyuan Formation, and Shanghuang quarry are approximately Lutetian in age, younger than Khaychin Ula. The Shara Murun and Heti Formation mammal faunas are probably Bartonian in age (Holroyd and Ciochon, 1994).

Our analysis shows that the Andarak fauna is most similar at the familial level with the Mongolian Khaychin Ula fauna. However, the taxa known from Khaychin Ula appear more derived than those from Andarak; therefore, we assume that Khaychin Ula is somewhat younger in age (possibly early Lutetian). Zoogeographically, the Andarak fauna belongs to a central Asian province, which was characterized by semi-arid to arid conditions, with predominantly open landscapes. Eastern China was in a different zoogeographic province, having a more humid climate and mainly forested and swampy landscapes. The latter region was an area of intensive intercontinental exchanges. North American faunal elements are conspicuously present in the Wutu fauna (Tong and Wang, 1994, 1995, 1998; Beard and Wang, 1995; Tong and Dawson, 1995). A third faunal province was spread along the Tethys border in southwestern Asia (the Kuldana and Subathu faunas). The absence of mixodontians and lagomorphs in these faunas probably reflects ecological factors, possibly forested environments. Endemic groups known from this province, such as Raoellidae, Anthracobunidae, and possibly Cetacea, may have differentiated on the Indian subcontinent and subsequently spread to the Asian mainland.

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APPENDIX

Distribution of 61 mammalian families* in selected Eocene localities in Asia.

Localities	Families
Shanghuang	10000 01110 00111 10000 00111 11000 01111 00101 11111 01000 01001 00101 1
Tsagan Khushu	01010 10010 00010 00000 10010 00000 00000 01000 00000 10011 10111 10000 0
Limuping	01000 00000 01100 00110 00000 00000 00000 01000 00000 10010 00010 00000 0
Lower Obayla	00000 00000 00011 00000 00000 00001 00000 01101 01000 01000 01011 01010 0
Yuhuangding	00000 00000 00110 00011 00000 00000 00000 00101 00010 00010 00011 00000 0
Andarak	00100 00000 10010 00000 00000 00010 00000 00110 01110 00001 01011 00000 0
Kuldana	00000 00000 00000 00000 00110 01011 10001 10111 00000 01100 00001 00000 0
Subathu	00000 00000 10010 00000 00000 00010 00000 11101 01000 01000 00001 00000 0
Khaychin Ula	00100 00000 10010 00010 00000 00000 10000 00110 01100 01000 01011 00000 0
Heti	00001 00000 10010 10000 00101 10000 10001 00110 00110 01000 00001 00100 0
Upper Lushi	00000 00001 10011 11010 01000 00001 10001 00111 01110 01000 01010 00000 0
Hetaoyuan	00000 00001 00011 00000 00000 00100 00000 00111 01100 01000 01000 00000 0
Ulan Shireh	00000 00000 11111 10110 00000 00000 10000 00110 01100 01000 01001 00000 0
Arshanto	00100 00000 11000 00111 00000 00000 00000 01111 01000 01000 00010 00000 0
Irdin Manha	00010 00001 11111 00010 00000 00000 10000 00111 01000 01000 00000 00000 0
Camp Margetts	00000 00001 10000 00000 00000 00000 00000 00111 01110 01000 00001 00000 0

* 0 designates taxon absent from locality; 1 designates taxon present at locality. From left to right, mammalian families are as follows: 1, Didelphidae; 2, Palaeoryctidae; 3, Micropternodontidae; 4, Pantolestidae; 5, Changlelestidae; 6, Nyctitheriidae; 7, Erinaceidae; 8, Chiroptera (family indet.); 9, Hyopsodontidae; 10, Arctocyonidae; 11, Mesonychidae; 12, Hapalodectidae; 13, Didymoconidae; 14, Hyaenodontidae; 15, Miacidae; 16, Canidae; 17, Felidae; 18, Pantolambdodontidae; 19, Coryphodontidae; 20, Uintatheriidae; 21, Arctosylopidae; 22, Stylinodontidae; 23, Tillotheriidae; 24, Omomyidae; 25, Tarsiidae; 26, Eosimiidae; 27, Adapidae; 28, Tupaiidae; 29, Diacodexeidae; 30, Dichobunidae; 31, Helohyidae; 32, Homacodontidae; 33, Leptomerycidae; 34, Entelodontidae; 35, Anthracotheriidae; 36, Raoellidae; 37, Isectolophidae; 38, Lophialetidae; 39, Deperetellidae; 40, Helaletidae; 41, Tapiridae; 42, Hyracodontidae; 43, Amynodontidae; 44, Eomoropidae; 45, Palaeotheriidae; 46, Equidae; 47, Brontotheriidae; 48, Anthracobunidae; 49, Eurymylidae; 50, Mimotonidae; 51, new family of Glires (see Dashzeveg et al., 1998); 52, Mytonolagidae; 53, Alagomyidae; 54, Tamquammyidae; 55, Chapattimyidae; 56, Ivanantoniidae; 57, Gliridae; 58, Cricetidae; 59, Zapodidae; 60, Ischyromyidae; 61, new family of Rodentia (Qi et al., 1996).

Note added in proof:

All North American material previously attributed to *Forstercooperia* was recently assigned to the new rhinocerotoid genus *Uintaceras* (Holbrook and Lucas, 1997).

HOLBROOK, L. T., AND S. G. LUCAS. 1997. A new genus of rhinocerotoid from the Eocene of Utah and the status of North American "*Forstercooperia.*" Journal of Vertebrate Paleontology, 19:384–396.

SYSTEMATIC REVIEW OF THE PAKICETIDAE, EARLY AND MIDDLE EOCENE CETACEA (MAMMALIA) FROM PAKISTAN AND INDIA

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ABSTRACT

Four cetaceans occur in the freshwater sediments of the Eocene Kuldana and Subathu formations of northern Pakistan and northwestern India: *Ichthyolestes pinfoldi, Pakicetus attocki, P. inachus,* and *Nalacetus ratimitus,* n. gen. and sp. These species form a distinct group of archaic cetaceans (archaeocetes) here classified as pakicetids. Dental and mandibular fragments are known for all pakicetids, but only one partial skull is available (the holotype of *P. inachus*) and no postcranials have been described. Pakicetids can only be characterized on the basis of a combination of primitive and derived features, and it is thus unclear whether the family forms a monophyletic group or a paraphyletic lineage segment. Possible synapomorphies of the ear region cannot be evaluated for all genera, and dental features known in all three genera cannot be studied phylogenetically because the cetacean sister group within archaic ungulates is unclear. Pakicetids are only known from Indo–Pakistan.

INTRODUCTION

Cetaceans abound in the early and middle Eocene sediments of the northern edge of Indo–Pakistan, and Gingerich et al. (1983) suggested that cetaceans originated there. Indo–Pakistan is the only area where the earliest and most plesiomorphic cetaceans, here called pakicetids, are found, and several other families of early cetaceans (protocetids, remingtonocetids, and ambulocetids) are known from this region as well. Pakicetids are only known from the Kuldana and Subathu formations of northern Pakistan and northwestern India.

Described cetaceans from the Kuldana Formation have been found in two areas. The first of these is in the Kala Chitta Hills (Punjab), where cetaceans have been recovered near the village of Ganda Kas (Dehm and Oettingen-Spielberg, 1958; Gingerich, 1977; West, 1980; Thewissen and Hussain, 1993; Thewissen et al., 1994). This area is sometimes called Lammidhan. Kuldana cetaceans are also known from a locality near the village of Chorlakki in North-West Frontier Province (Gingerich and Russell, 1981, 1990; Gingerich et al., 1983).

The Kuldana Formation includes a variety of lithologies. Low in the section it mainly consists of unconsolidated red and grey muds, with occasional small conglomerate lenses. These deposits represent fluvial environments: channel-lag deposits (the conglomerates) and overbank deposits (the mudstones). Wells (1984) called these beds the Lower Member of the Kuldana Formation, and their sedimentology was discussed by Wells (1983, 1984) and Aslan and Thewissen (1996). Three cetaceans have been named from this part of the formation: *Ichthyolestes pinfoldi* and *Pakicetus attocki* from the Kala Chitta Hills and *P. inachus* from Chorlakki.

The red and grey muds are followed by a varied succession of thin beds that include limestone, dolomite, mudstone, and sand. Wells (1983, 1984) called these the Upper Member of the Kuldana Formation and observed that they include freshwater and marine deposits. These beds have also been included in the Kohat Formation (Meissner et al., 1974) and have yielded one cetacean, *Gandakasia potens.* They are less fossiliferous than the Lower Member or the overlying marine beds.

The top of the Kuldana Formation represents a transgression, and consists of greenish-grey silts alternating with thin, discontinuous bivalve banks. The last silt bed is followed by a thick (more than 1 m) bivalve bank which Wells (1984) described as

the transition to the Kohat Formation. The remainder of the Eocene section in the Kala Chitta Hills consists of massive limestones with Foraminifera. One cetacean has been described from the top of the Kuldana: *Ambulocetus natans*. Thewissen et al. (1996) referred *Ambulocetus* and *Gandakasia* to Ambulocetidae.

Pilgrim (1940) considered the Kuldana Formation middle Eocene (lower Lutetian) in age on the basis of unspecified foraminiferal correlations with Europe. Dehm and Oettingen-Spielberg (1958) stated that it contained early or middle Eocene faunas, and that the middle Eocene age was more likely based on correlations to marine beds in the Sulaiman Range of central Pakistan and similarities of the mammals to middle Eocene Asian faunas. They did observe that the early Eocene faunas of Asia could not be compared, as so few taxa were known from them. A middle Eocene age for the Kuldana faunas was accepted by Gingerich (1977), Hussain et al. (1978), West and Lukacs (1979), and West (1980). Meissner et al. (1974) referred to the lower Kuldana Formation as the Crimson Clays of the Mami Khel Clay, and established an early Eocene age for these rocks based on the presence of early Eocene foraminifera in beds overlying the Crimson Clays in North-West Frontier Province. De Bruijn (1982) also considered it early Eocene, apparently on the basis of its rodent fauna. Gingerich and Russell (1981) proposed that the Kuldana Formation of North-West Frontier Province is near the early–middle Eocene boundary and may straddle it. Thewissen et al. (1987) noted that the eastern and western faunas could be diachronous. Gingerich and Russell (1990) concluded on the basis of sequence stratigraphy that the age of the Kuldana Formation is latest early Eocene, and found that the evidence from mammal fossils was consistent with this. We believe that all these data are most consistent with an early Eocene age for the Lower Member of the Kuldana Formation.

The Kuldana outcrops follow the east–west structural trend of the Himalayan chain. Near the border of Pakistani Punjab and Kashmir, this trend is interrupted by the Hazara–Kashmir syntaxis, which covers the Eocene outcrops. Eocene rocks crop out again east of the syntaxis, and stretch into Indian Kashmir and Himachel Pradesh. These are sediments of the Subathu Formation, which include both freshwater and marine deposits.

Cetaceans have been reported from the Subathu Formation of Pakistani Kashmir and from Indian Kashmir. Gingerich and Russell (1994) described three postcranial specimens from the Subathu Formation of Pakistani Kashmir. At least one of these, the Batala pelvis, probably represents a cetacean. One cetacean specimen was described as *Ichthyolestes* from the Subathu Formation of Indian Kashmir (Kumar and Sahni, 1985). An isolated tooth was described as a mesonychian, cf. *Honanodon*, by Ranga Rao (1973).

We collected new cetacean specimens in the conglomerates of the lower Kuldana Formation of the Kala Chitta Hills. These specimens add significantly to our understanding of early cetacean morphology and allow an evaluation of the described species. Until now, comparison of the lower Kuldana cetaceans has been problematic, because species were mainly known from their holotypes, and these could not be directly compared. Some of the confusion concerning the identities of the lower Kuldana cetaceans can be resolved on the basis of this new material.

Institutional abbreviations used in text are: BMNH, Natural History Museum, London, United Kingdom; H–GSP, Howard University, Geological Survey of Pakistan, specimens housed at GSP office in Islamabad, Pakistan; IPHG, Institut für Paläontologie und historische Geologie, Münich, Germany; ONG, Oil and Natural Gas Commission, Dehra Dun, India; UM, University of Michigan, Museum of Paleontology, Ann Arbor, Michigan; UM–GSP (also listed as GSP–UM), University of Michigan, Geological Survey of Pakistan, specimens housed at GSP office in Islamabad, Pakistan; VPL, Vertebrate Paleontology Laboratory, Panjab University, Chandigarh, India.

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758
Order Cetacea Brisson, 1762
Family Pakicetidae Gingerich and Russell, 1990

Pakicctinae Gingerich and Russell, 1990.
Pakicetidac Thewissen et al., 1996.

Type Genus.—*Pakicetus* Gingerich and Russell, 1981.

Referred Genera.—*Ichthyolestes* Dehm and Oettingen-Spielberg, 1958; *Nalacetus,* n. gen.

Age and Distribution.—Early to middle Eocene, northern Pakistan and northwestern India.

Diagnosis.—Cetaceans with palatine fissures present, nasal opening over the incisors, hypoglossal foramen present and well separated from jugular foramen. Paraconid and metaconid of molars present, but smaller than protoconid, talonid with hypoconid only. P^4 with three roots and a single cusp which is higher than the paracone of the molars. Upper molars with three cusps.

Description.—Known dental formula: 3.1.?.3/3.1.4.3. P^3 two-rooted. P^4 with high crown, a single cusp (paracone) and lingual bulge over third root. Upper molars with three main cusps, protocone lower than labial cusps, and lingual side of the tooth, especially trigon basin, reduced. M^1 smaller than M^2. P_{2-4} two-rooted, with the enamel extending further basally on the anterior and posterior side than it does in the central part of the tooth (yoke-shaped enamel outline). P_{2-4} with a single cusp (protoconid) that is triangular in labial view, and no talonid. dP_4 molarized. Lower molars lack trigonid basin and talonid basin. Trigonid dominated by protoconid, paraconid and metaconid small to absent. Concave anterior outline (re-entrant groove), talonid with a single cusp (hypoconid).

Discussion.—Although the first cetacean specimen from the Kuldana Formation was discovered more than half a century ago (BMNH M-15806), the cetacean affinities of this and other specimens were not recognized until the early 1980s (Gingerich cited in West, 1980; Gingerich and Russell, 1981). From then on, *Pakicetus*, *Gandakasia*, and *Ichthyolestes* were usually classified as protocetids. Kumar and Sahni (1986:329) included *Pakicetus* in a "family incertae sedis (probably new)," and Gingerich and Russell (1990) proposed inclusion of *Pakicetus*, *Ichthyolestes*, and *Gandakasia* in the subfamily Pakicetinae. Thewissen et al. (1996) transferred *Gandakasia* to Ambulocetidae and formally raised Pakicetinae to the family level.

Pakicetids resemble mesonychians in many aspects of their dentition. Dental similarities that are probably synapomorphies for Cete (mesonychians and cetaceans) include absence of trigonid basin (correlated with reduction of paraconid and metaconid) and absence of the talonid basin. All Cete are characterized by the small size of the trigon basin and talonid basin, and absence of the M_3 hypoconulid (Thewissen, 1994).

Mesonychians and pakicetids differ in other aspects of their dentition: the upper incisors and I_{2-3} of pakicetids are arranged anteroposteriorly, not mediolaterally, and are not juxtaposed (Prothero et al., 1988; Thewissen, 1994); P_{2-4} have enamel that reaches much further basally over the two roots than in the area between the roots, giving rise to the basally deeply indented (yoke-shaped) enamel profile

in lateral view; P^4 consists of a single cusp (paracone) that is higher than the paracone of the molars; the molar metaconid is posterolingual to the protoconid (in mesonychians it is absent or lingual). P_4 consists of a single triangular cusp that is much higher than the molars, whereas in mesonychians the protoconid is lower and additional cusps are present; the molar paraconid reaches high on the anterior side of the protoconid, it does not remain low on the cingulum as in mesonychians; and the anterior side of the molars is concave (the re-entrant groove of Ting and Li [1987], which also occurs in hapalodectids). Throughout the dentition, pakicetid molars have sharper crests and more gracile cusps than those of typical mesonychians.

Pakicetids differ from ambulocetids in having a single-rooted P_1 (and dP_1). This occurs in all examined pakicetid dentaries, but not in the holotype of *P. attocki* as described by West (1980). There is little doubt that the dental identifications of West are incorrect (see below), but this would not change the interpretation that P_1 is single rooted. This discrepancy cannot be resolved without further study of the specimen, which is lost.

We do not include *Gandakasia* in Pakicetidae. Little material is known for the taxon, and none of it was found in the redbeds of the lower Kuldana Formation. The type material described by Dehm and Oettingen-Spielberg (1958) and the material described by West (1980) from H–GSP Locality 58 (West and Lukacs, 1979) were found in beds overlying the redbeds. Morphological evidence suggests that *Gandakasia* is not a pakicetid (Thewissen et al., 1996), but instead is more closely related to *Ambulocetus*.

During our study of pakicetids, we also identified a number of cetacean specimens from northern Pakistan that have been described as pakicetids but pertain to a different family. Some of this material is ambulocetid, whereas other specimens are too fragmentary to be identifiable. Described ambulocetids from northern Pakistan include specimens reported in 1958 by Dehm and Oettingen-Spielberg (IPHG 1956 II 4, 5, and 6), in 1977 by Gingerich (UM 65868), in 1980 by West (H–GSP 497, 498, 499, and 500), in 1994 by Thewissen et al. (H–GSP 18472, 18473, 18497, and 18507), and by Thewissen et al. (1996, H–GSP 18474, 92148, and 92151). Other published and unpublished material of possible cetaceans from the Eocene of Indo–Pakistan can only be identified when more complete specimens become available (IPHG 1956 II 8 and 9; UM 65869; H–GSP 18391 and 18476; UM–GSP 1575,

1576, 1591; and ONG/K/19). Some of these specimens may not represent cetaceans.

Nalacetus, new genus

Type and Only Species.—*Nalacetus ratimitus*, n. sp.

Age and Distribution.—Early Eocene, redbeds of the lower Kuldana Formation, northern Pakistan.

Diagnosis.—Paracone of P^4 less than twice as high as the paracone of M^1. Lingual bulge of P^4 small. Protocone of upper molars robust, and metacone similar in size to paracone. Area between lingual and labial cusps of upper molars short mediolaterally. Strong paraconid on lower molars. Diastemata between C_1, P_{1-4}, and M_1 short or absent.

Discussion.—As explained in the specific discussion, *Nalacetus* combines aspects of *Pakicetus* and *Ichthyolestes* and is intermediate in size between the two (Fig. 1).

Etymology.—*Nala* (pronounced NAH-lah), Urdu for seasonally dry riverbed (wash or arroyo), referring to the type locality, which is the end of a dry riverbed. Also a reference to the nonmarine habitat of this genus. *Cetus*, Latin for whale.

Nalacetus ratimitus, new species
(Fig. 2C, D; 3C; 4G, K, L)

Pakicetus sp. (in part) Thewissen, 1993:fig. 9; Thewissen, 1994: fig. 2; Maas and Thewissen, 1995:fig. 1.

Holotype.—H–GSP 18521 (field number 92132), right P^4–M^1. Part of the holotype P^4 was preserved as an impression in matrix. This was cast in epoxy and attached to the original tooth.

Type Locality and Horizon.—H–GSP Locality 62 (West and Lukacs, 1979), redbeds of the lower Kuldana Formation, Kala Chitta Hills, Punjab, Pakistan.

Age and Distribution.—Type locality only, early Eocene.

Diagnosis.—As for the genus (currently monotypic).

Referred Material.—H–GSP Locality 62: H–GSP 18408 (P_x fragment, possibly P_3); H–GSP 91036 (mandible with fragment of C_1, P_{3-4}, trigonid of M_1, and alveoli for P_{1-2}); H–GSP 91044 (dP_4); H–GSP 91045 (M_x, probably M_2; talonid used for stable isotope analysis and enamel microstructure study).

Description.—P^4 (H–GSP 18521) with a single cusp (paracone) and three roots. Crown somewhat higher than M^1, although the actual tip is not preserved. Sharp crests extend anteriorly and posteriorly from the tip of the paracone, reaching the cingulum anteriorly and presumably posteriorly (this side of the tooth is damaged). Cingulum broad anteriorly, complete lingually, and interrupted posteriorly. Lingual cingulum bulges over the lingual

root, giving the tooth a triangular outline in occlusal view, but there is no protocone.

M^1 (H–GSP 18521) with three high cusps. Tip of protocone missing, but cusp is high and bulbous, weak metacrista present, and paracrista even weaker, no lingual cingulum. Protocone anterior in position, at the same level as the paracone. Trigon basin narrow mediolaterally. Cingulum barely present. Tips of paracone and metacone are not preserved, but they were higher than the protocone.

The dentary (H–GSP 91036, Fig. 3) is wide and tapers slightly: depth is 25 mm below P_4, and 21 mm below P_1, width at M_2 is 10.7 mm. The mandibular symphysis extends posteriorly to the posterior side of P_2. The base of the lower canine is preserved in H–GSP 91036, its anteroposterior length and its labiolingual width are both 9.2 mm. The canine has strong longitudinal enamel folds and a large cingulid posteriorly.

H–GSP 91036 is a juvenile with erupted M_1, and erupting P_{3-4}. The diastema between the canine and P_1 is 6 mm, and no other diastemata are present. Diastemata in this juvenile specimen are short and may not be representative for those of the adult, but they probably remained shorter than in *Pakicetus*. The distance between canine and M_1 is 78 mm. P_1 has one root; its alveolus is 9.2 mm long. P_2 has two roots; length between the extremes of its alveoli was approximately 16 mm. The base of P_3 is not visible. It has a single cusp (protoconid) and is triangular in lingual view. Sharp crests extend from its tip to the anterior and posterior cingulids. The angle between these crests is more than 50°.

P_4 (H–GSP 91036) is similar to P_3, bearing a single cusp that is triangular in side view. It has a strong anterior cingulid that lacks cusps. It has a faint lingual cingulid, and the enamel reaches much further in the central part of the tooth than anteriorly and posteriorly. The crests extending from the protoconid have fine crenulations, and the angle between them is more than 50°. There is no talonid.

dP_4 (H–GSP 91044) has thin enamel and is dominated by the large protoconid. The crest that extends from the tip of the protoconid to the anterior cingulid divides near the base of the tooth, giving rise to a slight bulge in the contour, the paraconid. The anterior cingulid is strong, with stylids labially and lingually, giving the anterior cingulid a concave outline in occlusal view. The lingual side of the protoconid bears shallow longitudinal enamel creases. A crest also extends from the protoconid posteriorly, crossing the metaconid and hypoconid. These cusps are well developed. There is no talonid basin. Approximate length of H–GSP 91044 dP_4 is 18.1 mm, and width is 5.4 mm.

The trigonid of the lower molar (H–GSP 91045, total length: 16.5 mm, width: 6.7 mm) is dominated by the large protoconid. The paraconid is smaller and fused to the anterolingual side of the protoconid. The metaconid is smaller than the paraconid and situated posterolingually. There is no trigonid basin. The talonid also lacks a basin. It bears a single cusp (the hypoconid), which has steep sides and distinct crests extending to the trigonid (cristid obliqua) and the posterior cingulid. The anterior cingulid is strong and flares lingually and labially, giving rise to a concave anterior side (re-entrant groove of Ting and Li, 1987). Labial and posterior cingulids are present, but weak. Apical wear is strong on this tooth, exposing a low bulge of dentine on the trigonid. H–GSP 91045 is probably an M_2, given its larger size (length at the roots is 15.5 mm) than M_1 of H–GSP 91036 (11.2 mm at the roots). Few features are preserved on the M_1 of H–GSP 91036. It is similar to H–GSP 91045, and preserves the large paraconid.
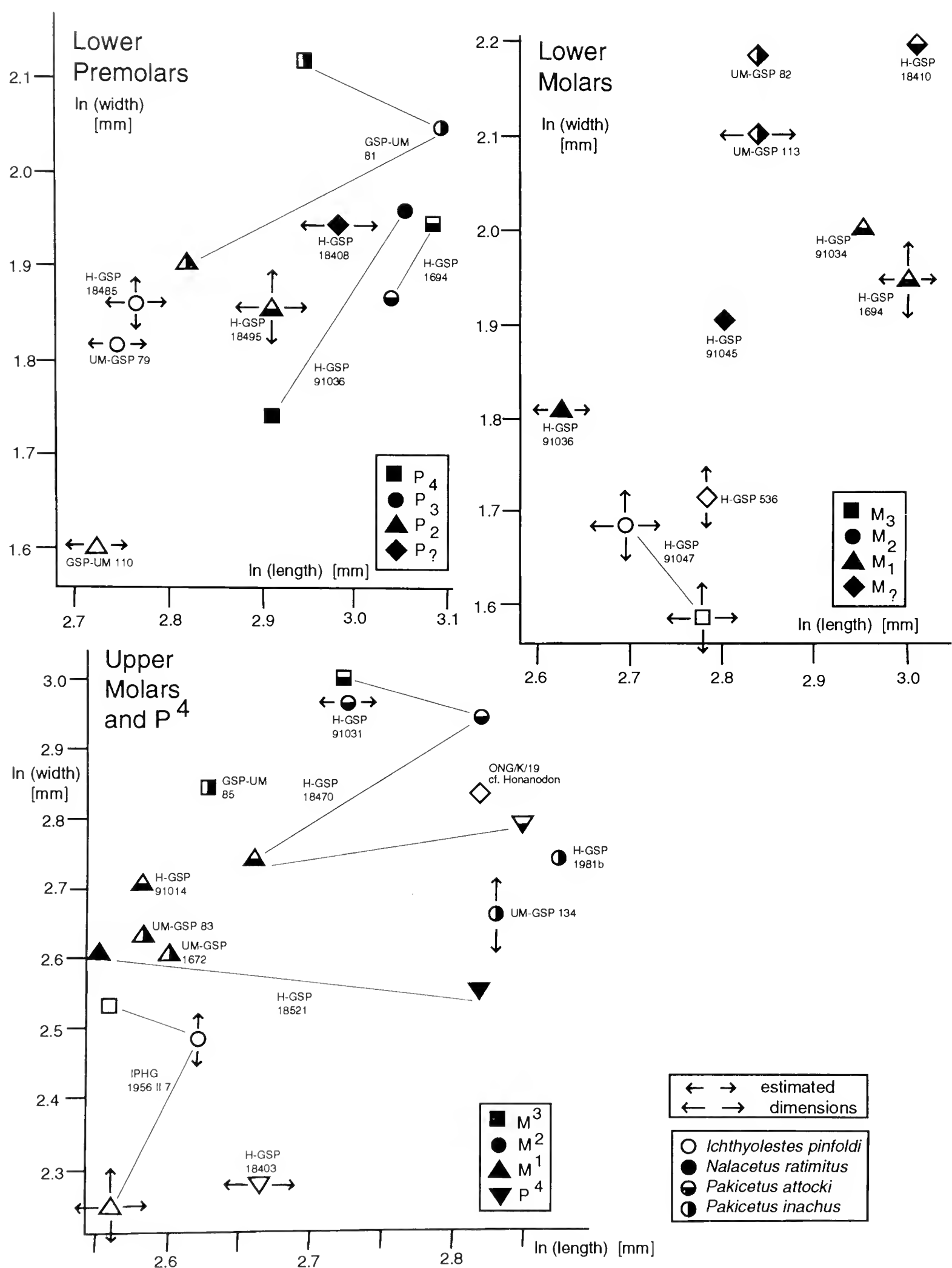
Discussion.—We chose a damaged maxilla with

Fig. 1.—Bivariate plots of pakicetid cheek-tooth dimensions, combining specimens from all localities. Lines connect teeth in the same jaw, short and long arrows indicate close and gross estimates.
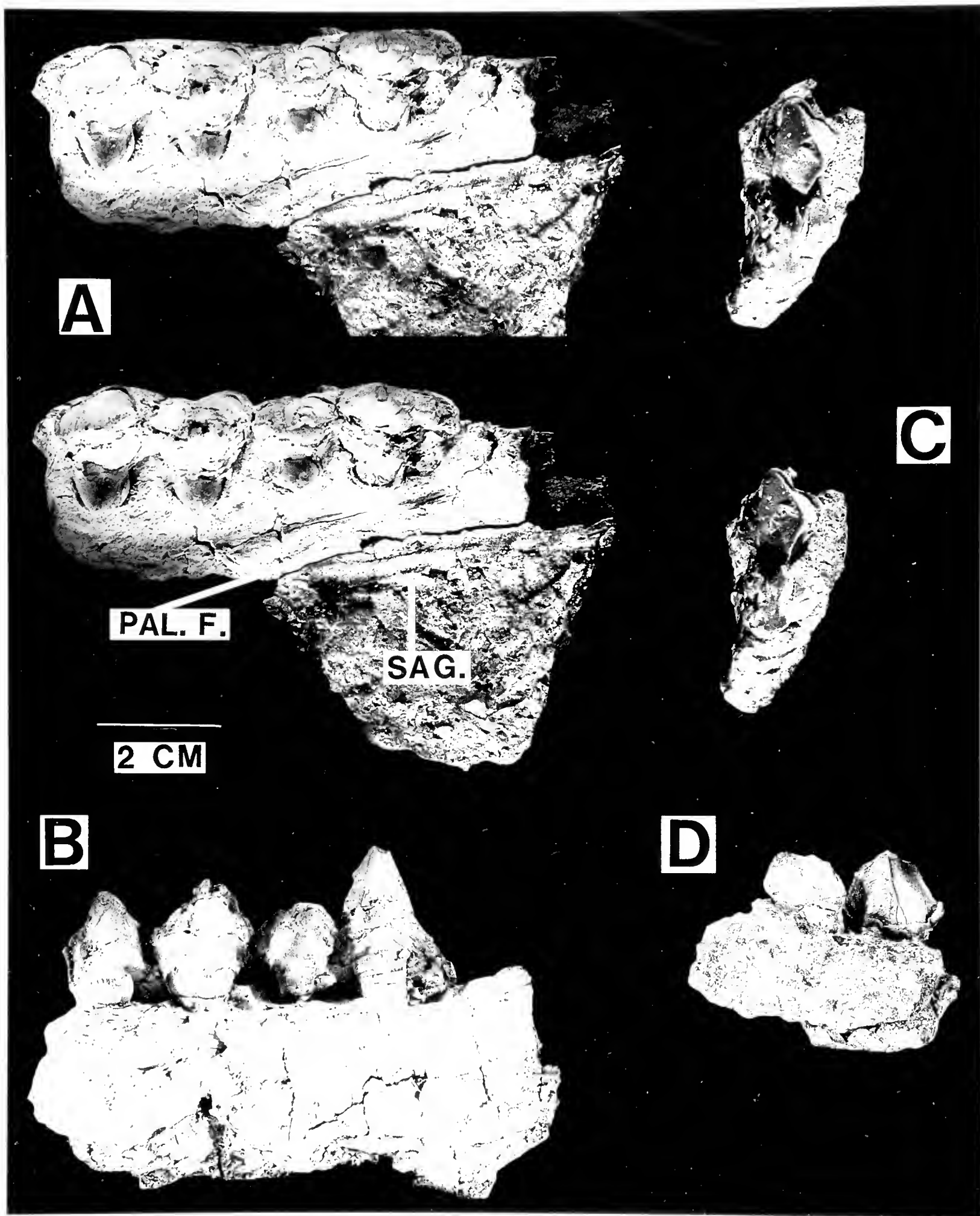
Fig. 2.—A, B. Right maxilla of *Pakicetus attocki* preserving P¹–M³ (H–GSP 18470) in occlusal (A) and lingual (B) views. Occlusal view is stereopair. Note palatine foramen (PAL. F.). Lingual edge of specimen represents sagittal plane (SAG.). C, D. Right maxilla of *Nalacetus ratimitus*, n. gen. and sp., preserving P¹–M³ (H–GSP 18521, holotype) in occlusal (C) and lingual (D) views. Occlusal view is stereopair.
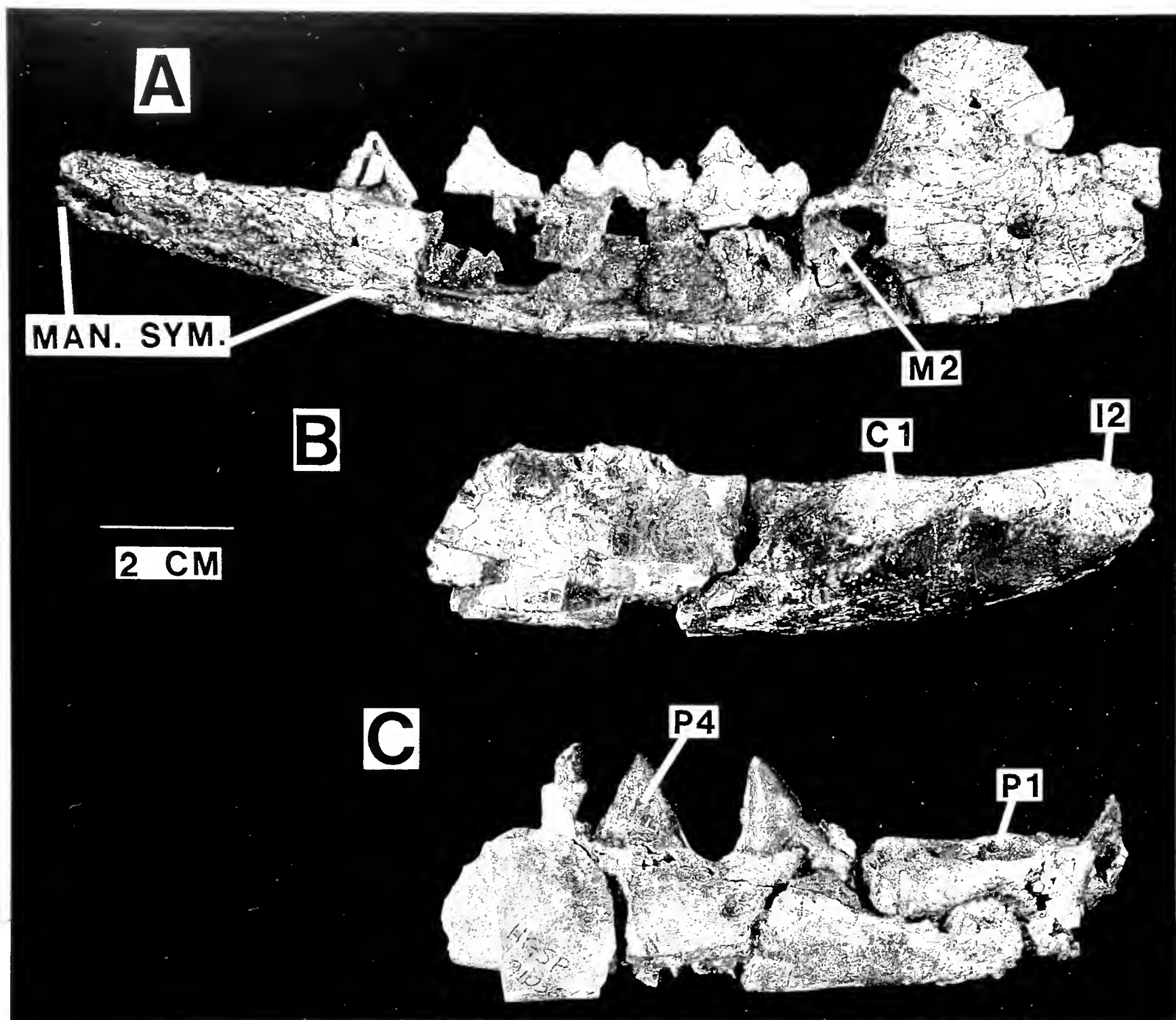
Fig. 3.—A. Juvenile right dentary of *Pakicetus attocki* preserving dP$_{2-4}$, M$_1$, and unerupted fragment of M$_2$ (H–GSP 91034) in lingual view. Note that the mandibular symphysis (MAN. SYM.) extends to dP$_3$, and the unerupted M$_2$, visible through window in jaw. B. Anterior dentary of *Pakicetus attocki* (H–GSP 18495) in labial view, showing roots of P$_2$ and alveoli for I$_2$–P$_1$. C. Juvenile right dentary of *Nalacetus ratimitus*, n. gen. and sp., preserving base of C$_1$, P$_{3-4}$, and trigonid of M$_1$ (H–GSP 91036) in labial view.

P^4–M^1 as the holotype because its molar can be compared with the holotype of *Ichthyolestes pinfoldi* (which preserves M$^{2-3}$), and with an important referred specimen of *Pakicetus attocki* (H–GSP 18470).

Nalacetus ratimitus is larger than *Ichthyolestes pinfoldi* and smaller than *Pakicetus attocki* and *P. inachus*. This is most obvious in the upper and lower molars (Fig. 1). The upper molars of the three pakicetid genera from the lower Kuldana Formation differ most with respect to the molar protocone. This cusp is slender in *Ichthyolestes*, is placed in the middle of the tooth, and lacks cristae. In *Nalacetus*, this cusp is robust, displaced anteriorly, and

has weak cristae. In *Pakicetus*, it is robust, displaced posterolingually (giving rise to a broad trigon basin), and it has stronger cristae, especially the paracrista.

Lower molars of *Nalacetus* can best be identified on the basis of the large paraconid (H–GSP 91036 and 91045). Isolated lower premolars are similar to those of *Pakicetus* and are easily confused; H–GSP 18408 was referred on the basis of its similarity in size and robusticity to H–GSP 91036. Dentaries of the three genera also differ. The dentaries of *Pakicetus* (H–GSP 18495 and 91034) and *Nalacetus* (H–GSP 91036) are wide, whereas those of *Ichthyolestes* (H–GSP 18485, 91015, and 91047) are narrow

and deep. *Ichthyolestes* and *Nalacetus* have dentaries that barely taper rostrally, unlike that of *Pakicetus*. An isolated dP$_4$ (H–GSP 91044) differs from those of *Ichthyolestes* (H–GSP 18395 and 91047) and *Pakicetus* (H–GSP 91034) in size and in the presence of a long protoconid and small paraconid. This suggests that the specimen represents *Nalacetus*. dP$_4$ of *Nalacetus* and *Ichthyolestes* have a short, sharply angled triangular profile, whereas that of *Pakicetus* is longer and lower. *Ichthyolestes* lacks stylids on the anterior cingulid of dP$_4$.

Etymology.—Latinized from "rati miti," which means "red earth" in the local Potwari dialect of the Punjabi language. This indicates the color of the sediments in which the new species is found, and is suggestive of the depositional environment.

Ichthyolestes Dehm and Oettingen-Spielberg, 1958

Ichthyolestes Dehm and Oettingen-Spielberg, 1958:15; Szalay and Gould, 1966:151.

Type and Only Species.—Ichthyolestes pinfoldi Dehm and Oettingen-Spielberg, 1958.
Age and Distribution.—Early Eocene, redbeds of the lower Kuldana Formation, northern Pakistan.
Differential Diagnosis.—Paracone of P^4 higher than in *Nalacetus*. Lingual bulge of P^4 smaller than in *Nalacetus* and *Pakicetus*. Protocone slender, unlike *Pakicetus attocki* and *Nalacetus*. Protocone of upper molars close to labial cusps, unlike *Pakicetus*. Protoconid of premolars narrow. M$^{1-2}$ metacone large, unlike *Pakicetus*. P$_2$ with sharply angled tip, unlike *Pakicetus*. Molar paraconid much smaller than in *Nalacetus*. Trigonid of molars longer (anteroposteriorly) than in *Nalacetus* and *Pakicetus*.
Discussion.—The typodigm material of *Ichthyolestes* consists of only two fragmentary specimens, but it led Dehm and Oettingen–Spielberg (1958) to believe that *Ichthyolestes* was a fish eater. This insight, reached long before the cetacean nature of the specimen was recognized, may be correct.

Ichthyolestes pinfoldi Dehm and Oettingen-Spielberg, 1958
(Fig. 4F, H; 5)

Ichthyolestes pinfoldi Dehm and Oettingen-Spielberg, 1958:15, fig. 2, pl. 1.5; Szalay and Gould, 1966:151; Gingerich and Russell, 1990:15, fig. 9.
Creodontium gen. and sp. indet. (*Ichthyolestes?*), Dehm and Oettingen-Spielberg, 1958:17, pl. 1.1.
Basilosauridae indet., West, 1980:517, fig. 2.2.
Protocetidae indet., West, 1980:516, fig. 2.3.
Pakicetus attocki (in part), Gingerich and Russell, 1981:243; 1990:14.
Pakicetus inachus (in part), Gingerich and Russell, 1990:3, fig. 6I–L, 7.

Ichthyolestes or *Pakicetus*, Gingerich and Russell, 1990:6, fig. 1E.
Pakicetus sp. (in part) Thewissen, 1993:fig. 9.

Holotype.—IPHG 1956 II 7, maxilla with M$^{2-3}$ as stated in the type description. Gingerich and Russell (1990) noted the broad separation of alveoli for the tooth anterior to the two preserved crowns and concluded that these alveoli most likely represented dP^4 and that the preserved crowns were M$^{1-2}$. Instead, we take the alveoli to be narrow because only their apex is preserved (the alveolar rim of the maxilla is missing), and agree with the type description that the preserved crowns are M$^{2-3}$. The last tooth in the jaw has a reduced posterior side (weak metacone) and proportions very similar to those of M^3 in *Pakicetus*. Gingerich and Russell (1990) also noticed a fragment of the germ of P^4 over the alveolus for the most anterior tooth. This fragment is clearly displaced, as the tip of the cusp faces caudally and is thus at right angles to its post-eruptive position.
Type Locality.—Locality 21 of Dehm and Oettingen-Spielberg (1958). West and Lukacs (1979) identified this as H–GSP Locality 220.
Age and Distribution.—Early Eocene, redbeds of the lower Kuldana Formation, northern Pakistan.
Diagnosis.—As for the genus (currently monotypic).

Referred Specimens.—Locality 24 of Dehm and Oettingen-Spielberg (1958): IPHG 1956 II 9 (probably dP$_3$). H–GSP Locality 62: H–GSP 536 (M$_x$); H–GSP 18395 (dP$_4$); H–GSP 18403 (partial P^4); H–GSP 18485 (dentary with erupting C$_1$, unerupted P$_{2-4}$, and alveoli for P$_1$ and M$_1$ [P$_{2-3}$ have been removed from their crypts]); H–GSP 91015 (dentary with alveoli for [d]I$_{1-2}$, erupting I$_3$ and C$_1$, alveolus for P$_1$, unerupted P$_2$ [incorrectly glued], and P$_3$ in its crypt); H–GSP 91047 (dentary with ascending ramus, dP$_4$, unerupted and partially visible M$_3$, fragment of P$_2$, and alveoli for I$_3$, C$_1$, dP$_3$, and M$_{1-2}$); H–GSP 92159 (anterior fragment of dP$_4$). Unknown locality in the Ganda Kas area (see West, 1980): H–GSP 1974a (not seen). Locality Chorlakki: UM–GSP 79 (probably P$_2$); UM–GSP 110 (probably P$_2$); UM–GSP 1936 (upper premolar, not P^4). Tentatively referred specimens from Chorlakki: UM–GSP 1411, 1534, 1546, and 1553 (described by Gingerich and Russell, 1990).

Description.—The only known P^4 (H–GSP 18403) retains little enamel. The paracone is high, and the enamel of its labial side is clearly yoke-shaped. The postparacrista is worn off, exposing a broad band of dentine. There is no protocone, but the enamel bulges lingually over the lingual root. Enamel here is crenulated and there is a weak posterior cingulum. The lingual
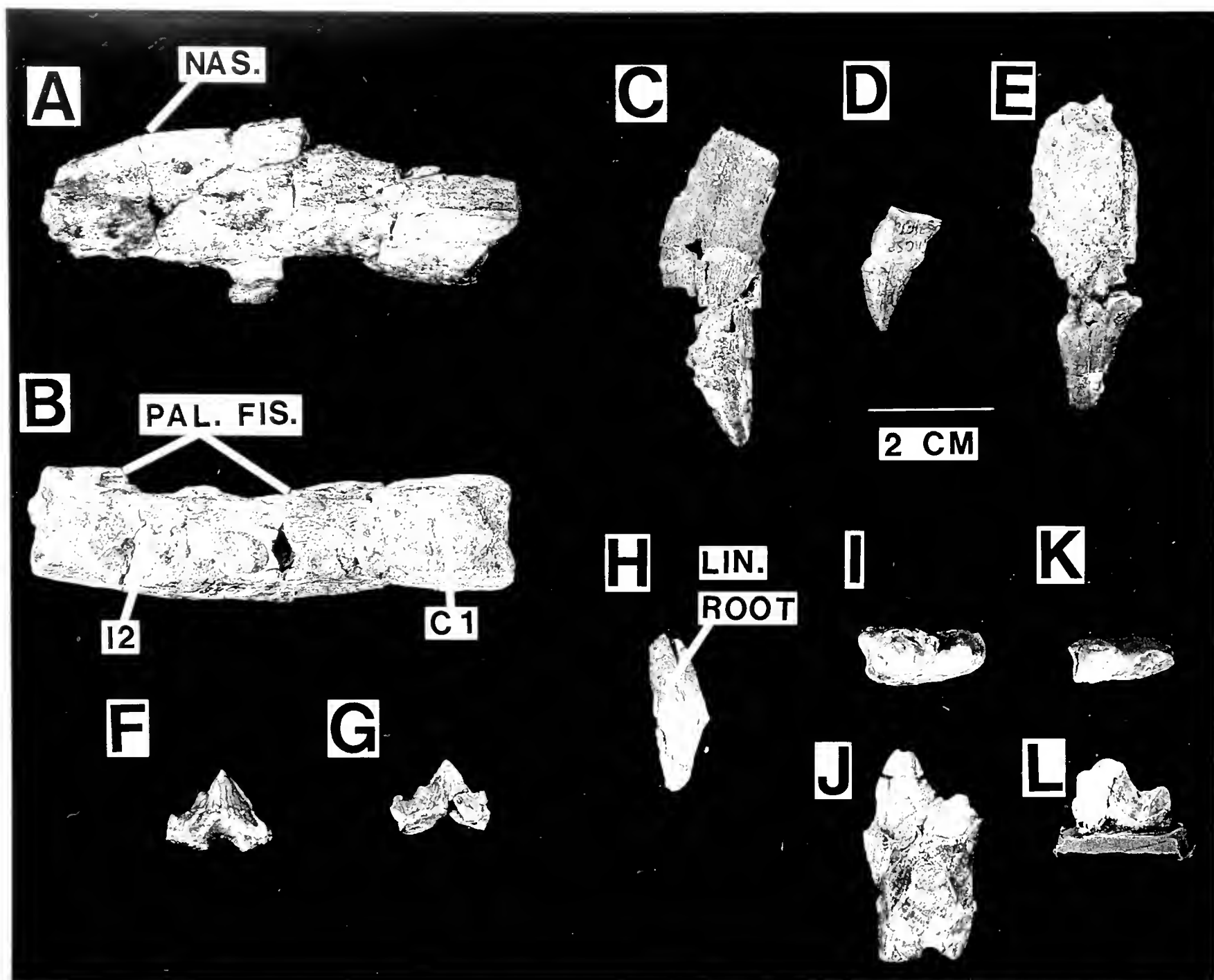
Fig. 4.—A, B. Premaxilla of *Pakicetus attocki* preserving crown of I^3 and alveoli for I^2 and C^1 (H–GSP 18467) in lingual (A) and occlusal (B) views. Note convexity indicating anterior contact of nasals (NAS.), and palatine fissure (PAL. FIS.). C–E. Presumed C^1 (H–GSP 18519), I^1 (H–GSP 91030), and P^2 (H–GSP 18399), respectively, of *Pakicetus attocki*. F, G. dP_4 of *Ichthyolestes pinfoldi* (H–GSP 18395) and *Nalacetus ratimitus*, n. gen. and sp., (H–GSP 91044), respectively, in lingual view. H. P^4 of *Ichthyolestes pinfoldi* in lingual view (H–GSP 18403). Note root under lingual bulge (LIN. ROOT). Approximately two-thirds of the crown is preserved. I, J. M_x of *Pakicetus attocki* (H–GSP 18410) in occlusal (I) and labial (J) views. K, L. M_x of *Nalacetus ratimitus* (H–GSP 91045) in occlusal (K) and labial (L) views.

part of the crown is set much deeper into the palate than the labial part.

The protocone of the upper molars (IPHG 1956 II 7) is more or less in the middle of the tooth. There is no trigon basin, causing the enamel at the base of the labial and lingual cusps to meet at a steep anteroposterior furrow. Paracrista and metacrista are weak. Paracone and metacone of M^x are approximately similar in size. M^x has a weak anterior and posterior cingulum. The metacone of M^x is greatly reduced in size, and the tooth lacks a parastyle. Its protocone is slender and lacks cristae, as in M^x. Only alveoli for M^x are preserved in the type specimen and these form the basis for the size estimate of Figure 1.

The dentary (H–GSP 18485, 91015, and 91047) is narrow labiolingually and retains the same depth over its entire preserved length (H–GSP 91047: maximum width at M_2 8.4 mm, at I_x 7.2 mm; depth at both 27 mm; length between C_1 and M_1 75 mm.

H–GSP 91015: maximum width at C_1 8.7 mm. H–GSP 18485: length between C_1 and M_1 81 mm). The maximum diameter of the mandibular foramen of H–GSP 91047 is 7.8 mm, and the mandibular symphysis reaches posteriorly to P_2 (H–GSP 18485 and 91047).

The entire incisor area is preserved in H–GSP 91015. $I_{1,2}$ are arranged mediolaterally in the dentary. I_x is posterior to I_2. Alveoli for I_2 (or dI_2) and dI_x are separated by a diastema of 8 mm. Judging from the alveoli, I_1 is the smallest and I_2 is the largest incisor, the diastema posterior to I_x is approximately 9.5 mm. I_x and C_1 are erupting (H–GSP 91015), both are pointed, strongly conical and high, and implanted at a low angle (procumbent). Crown height (root to tip) cannot be determined, but it is much larger than crown length along the enamel–dentine junction (craniocaudal). They are similar in size. The (unerupted) base of C_1 is preserved in H–GSP 18485, the canine is long and slender,
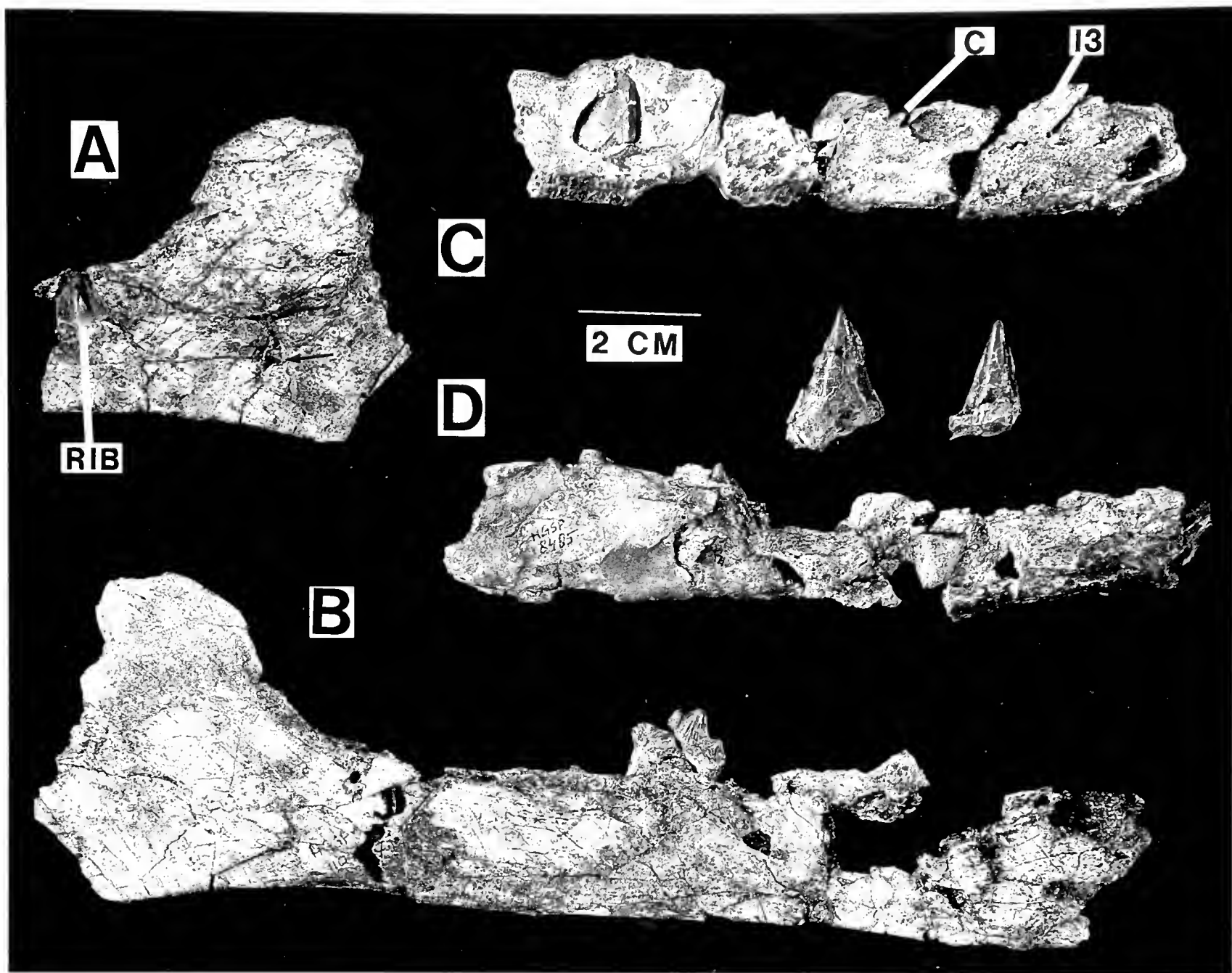
Fig. 5.—Dentaries of *Ichthyolestes pinfoldi*. A, B. Right dentary (H–GSP 91047) in lingual (A) and labial (B) views. Note mandibular foramen, indicated by black arrow, and unerupted M_3 with lingual rib (RIB) on trigonid. C. Right dentary (H–GSP 91015) in labial view with unerupted P_3 visible through window in jaw, unerupted C_1, and erupting I_3. D. Right dentary (H–GSP 18485) in labial view, with unerupted P_{2-4}. P_{2-3} were removed from the jaw.

with a flat lingual side and a convex labial side. The length at the base of the canine is 8.1 mm, and its width 6.1 mm. The alveolus for C_1 (H–GSP 91047) is 9.3 mm long and 4.8 mm wide. The alveolus for P_1 (H–GSP 18485: length 8.4 mm, width 6.3 mm) indicates that it was single rooted, possibly resembling the canine, but implanted more vertically.

Two small alveoli occur in the area of H–GSP 91015 above the unerupted P_2, these indicate that dP_2 was two rooted. The distance between the extremes of these alveoli is 7.9 mm. Fragments of P_2 are preserved in H–GSP 18485, 91015, and 91047. This tooth is two rooted, yoke-shaped, and has a high conical tip. Unlike most other pakicetid premolars, the angle at its tip is sharp, less than 40°.

P_3 (H–GSP 18485 and 91015) was also yoke-shaped and has a sharp tip. P_4 is similar to P_3; its base is not preserved in H–GSP 18485. P_{2-3} have weak lingual cingulids. The summits of P_{3-4} are less pointed than in P_2. The position of P_{2-4} (H–GSP 18485) in the jaw suggests that diastemata between them were short after eruption. This individual is not full grown and the alveoli may not be fully developed. No diastema followed P_4. In

H–GSP 91047, the alveolus between dP_2 and dP_3 is 7.6 mm. The maximum length between the alveoli of dP_3 is 11.5 mm.

Dehm and Oettingen-Spielberg (1958) described a two-rooted tooth (IPHG 1956 II 9; Gingerich and Russell, 1990:fig. 1E) with one large cusp as possibly representing *Ichthyolestes*. This tooth has a high protoconid, triangular profile, and crests extending to the anterior and posterior cingulid. The posterior crest runs over a second cusp which is smaller than the protoconid. The tooth is yoke-shaped and its thin enamel indicates that it was deciduous. It is less molarized than dP_4, and its size matches the alveoli for dP_3 in H–GSP 18485. Morphologically, it differs from the dP_3 of *Pakicetus* (H–GSP 91034) in the presence of two cusps. Its small size suggests that it pertains to *Ichthyolestes*. West (1980) described another deciduous premolar (H–GSP 1974a), which is very similar to IPHG 1956 II 9, and slightly smaller. It, too, probably represents *Ichthyolestes*.

dP_4 (H–GSP 91047) is 17.2 mm long and 4.0 mm wide and has thin enamel. It has a large protoconid and a low paraconid. The latter is anterior to the protoconid and connected to it by a crest. The metaconid is posterior to the protoconid, it is high and

connected by sharp crest. The trigonid is 12.1 mm in length. The talonid has a large hypoconid. The cingulid extends all around the trigonid and on the lingual side of the hypoconid. There is no re-entrant groove on dP$_4$. Two isolated dP$_4$s (H–GSP 18395: length 16.7 mm, width 4.0 mm; H–GSP 92159: width 3.5 mm) are similar to H–GSP 91047.

A lower molar (H–GSP 536) has a high protoconid, small anterolingual paraconid, and small posterolingual metaconid. The paraconid and metaconid are small bulges near the summit of the protoconid. Immediately lingual to the protoconid is a small fold of enamel that extends from the cingulid to the level of paraconid and metaconid and ends in a low bulge. This fold is smaller than the paraconid. The cristid obliqua slopes gently down the posterior side of the trigonid, lengthening the trigonid at its base. The talonid rises slightly above the cristid obliqua.

The trigonid of an unerupted M$_3$ (H–GSP 91047) is visible through a break in the dentary, and matches H–GSP 536 in morphology. The trigonid of the lower molars is long, and the paraconid small. M$_3$ of H–GSP 91047 also has a fold of enamel lingual to the protoconid; this enamel crest is larger and reaches higher up the protoconid than does the paraconid. The alveolus for M$_1$ (H–GSP 91047) is 16.7 mm long, that for M$_2$ 15.0 mm.

Discussion.—*Ichthyolestes* is the smallest pakicetid and had pointed teeth and a narrow jaw, indicating that its jaws were not forceful. Combined, the three mandibles that are known for *Ichthyolestes* (H–GSP 18485, 91015, and 91047) indicate that *Ichthyolestes* had a long and slender jaw, in spite of its small ascending ramus. All three preserve fragments of P$_2$, and in all three the eruption stage of this tooth is similar: its tip projects slightly above the alveolus. On the other hand, whereas the P$_3$ and P$_4$ of H–GSP 18485 are nearly formed in the jaw, there is hardly a trace of these teeth in H–GSP 91047.

Known lower molars of *Ichthyolestes* (and to a lesser extent its dP$_4$) have an enamel fold immediately lingual to the protoconid. This fold extends up the protoconid from the cingulid between the paraconid and the metaconid and, based on the small amount of material available, is absent in the lower molars of *Pakicetus* and *Nalacetus* (but present in the dP$_4$ of *Nalacetus*). In mesonychians, the metaconid is in this position, but it is unclear whether this similarity between *Ichthyolestes* and mesonychians is phylogenetically relevant. Lower molars of *Ichthyolestes* (H–GSP 536 and 91047) can also be identified on the basis of their long trigonid and small paraconid.

P$_2$ of *Ichthyolestes* is very diagnostic (H–GSP 18585 and 91047). It is two rooted and yoke-shaped, and its tip forms a sharp angle (less than 40°). This is unlike *Pakicetus* (UM–GSP 81) and *Nalacetus* (H–GSP 91036), in which the tip of P$_2$ forms a much greater angle.

The P$_4$ (H–GSP 183403) was identified on the

basis of size; it is smaller than the P$_4$s known for *Nalacetus* and *Pakicetus*, and also differs morphologically. dP$_4$ of *Ichthyolestes* (H–GSP 18395 and 91047) is narrower and shorter anteroposteriorly than in *Pakicetus*. It differs from that of *Nalacetus* in the absence of styles on the anterior cingulum. Gingerich (1977) referred an unerupted fragmentary premolar (UM 65869) to *Ichthyolestes pinfoldi*. He estimated the length of this specimen as 11 mm, substantially less than other *Ichthyolestes* premolars (H–GSP 18485). Gingerich and Russell (1990) excluded this specimen from *Ichthyolestes*, and we concur.

Two teeth from Chorlakki represent P$_2$s of *Ichthyolestes*. Gingerich and Russell (1990) described UM–GSP 110 as a P$_1$ of *Pakicetus inachus* based on their comparison with P$_{2-4}$ of this species and other isolated teeth. They implied that a large size difference exists between P$_1$ and P$_2$, whereas we consider it more likely that two taxa are represented. Moreover, pakicetid jaws from the Kala Chitta Hills indicate that P$_1$ is single rooted. UM–GSP 79 is yoke-shaped and has thick enamel, indicating that it is not a deciduous premolar (as previously observed by Gingerich and Russell, 1990). It does match P$_2$ of *Ichthyolestes* (e.g., H–GSP 18485) in morphology and shape. Gingerich and Russell (1990) described UM–GSP 79 as an upper canine of *Pakicetus inachus*. This tooth has a slender crown, and two roots that are close. H–GSP 18467 shows one large rounded alveolus for the upper canine of *Pakicetus attocki*. The shape of its alveolus does not match that of UM–GSP 79. The alveolus of H–GSP 18467 is 14.1 mm long and 12.0 mm wide, whereas UM–GSP 79 is 12.5 mm long across both roots and only 5.9 mm wide. These features suggest that this tooth is not the canine of an animal similar to *Pakicetus attocki*. Alternatively, this tooth is very similar to the P$_2$ of *Ichthyolestes pinfoldi*. Its tip is sharply angled, less than 40°, unlike the P$_{2-4}$ of *Pakicetus*.

UM–GSP 1936 is an upper premolar from Chorlakki described as P^1 by Gingerich and Russell (1990). A maxillary fragment of *Pakicetus attocki* (H–GSP 18467) indicates that the width of the bilateral rostrum at C^1 is more than 39 mm. A maxillary fragment attached to UM–GSP 1936 indicates that the rostrum was only 28 mm, suggesting that this specimen represents a much smaller species. This and the slender crown suggest that it is most likely *Ichthyolestes*. No maxilla is known for this taxon and the tooth may represent any locus from P$^{1-3}$. These specimens from Chorlakki establish the

occurrence of *Ichthyolestes* outside the Kala Chitta Hills.

Four additional teeth may also represent *Ichthyolestes* from Chorlakki. Gingerich and Russell (1990) described UM–GSP 1534 as a probable upper incisor. We agree with this identification, but the specimen does not fit the alveoli of a premaxilla of *Pakicetus attocki* (H–GSP 18467). Given that the cheek teeth of *Pakicetus attocki* and *P. inachus* are similar in size, this incisor probably represents a different genus. Upper incisors of *Pakicetus* (I^3 in H–GSP 18467) appear to have short crowns, whereas that of UM–GSP 1534 is long. The tooth is too small to be I_{2-3} of *Pakicetus*, and is not I_1 because its root is curved. It probably represents *Ichthyolestes*. A similar argument can be made for UM–GSP 1546.

UM–GSP 1411 and 1553 were described as C_1 by Gingerich and Russell (1990). These teeth are too small to fit the canine locus of the maxilla or the dentary of *Pakicetus* (H–GSP 18467 and 18495). They probably represent canines of *Ichthyolestes*.

Pakicetus Gingerich and Russell, 1981

Protocetus, (in part) West, 1980.
Pakicetus Gingerich and Russell, 1981:238; 1990:3.

Type Species.—*Pakicetus inachus* Gingerich and Russell, 1981.

Included Species.—*Pakicetus attocki* (West, 1980).

Age and Distribution.—Early and middle Eocene redbeds of the lower Kuldana Formation (northern Pakistan) and Subathu Formation (northwestern India).

Differential Diagnosis.—Paracone of P^4 much higher than paracone of the molars, unlike *Nalacetus*. Basal outline of P^4 much larger than M^1, unlike *Nalacetus*. Paracone of upper molars much larger than metacone, unlike *Nalacetus* and *Ichthyolestes*. Protocone placed lingually, giving rise to a wide trigon basin, unlike *Nalacetus* and *Ichthyolestes*. Angle at tip of protoconid of P_2 is more than 50°. Paraconid of molars much smaller than in *Nalacetus*, and trigonid higher.

Discussion.—The diagnosis of *Pakicetus* is based mainly on referred specimens of *P. attocki*. Although more or less generally acknowledged as the oldest and most primitive cetacean, *Pakicetus* is problematic taxonomically. The holotype of its type species is a braincase, which cannot be compared directly with the holotype (or nearly all referred material) of *Pakicetus attocki* or any material of other

pakicetids. Gingerich and Russell (1981) diagnosed *Pakicetus* as well as its type species mainly on the basis of referred dental material from the type locality (Chorlakki), on the assumption that only one cetacean occurred there. Improved understanding of the morphology of *Pakicetus attocki* and *Ichthyolestes pinfoldi* implies that *Ichthyolestes* also occurs at Chorlakki, leaving some doubt as to whether the holotype and referred specimens represent the same species. On the other hand, consistent with the hypothesis of Gingerich and Russell (1990), the improved collections do indicate the presence of a large common cetacean at Chorlakki that is distinct from the common cetaceans at H–GSP Locality 62. However, its generic name leaves some room for doubt because the type specimen of *P. inachus* might be conspecific with the dental holotype of *Ichthyolestes*. This in turn raises doubts about the generic attribution of *P. attocki*.

Based on the available evidence, and until more material is collected (associated dental material at Chorlakki and cranial material in the Kala Chitta Hills), we retain the concept of *Pakicetus* and its species as described by Gingerich and Russell (1981, 1990). We assume that most of the described molars and the lower jaw (UM–GSP 81) from the type description of *P. inachus* pertain to the taxon for which a braincase is known (UM–GSP 84). We also retain the concept of *Pakicetus attocki* as described by West (1980) and its generic attribution by Gingerich and Russell (1981, 1990): *P. attocki* is the most common, large pakicetid in the lower Kuldana Formation of the Kala Chitta Hills.

Stability is best served by retaining the two species of *Pakicetus* in the same genus. In both species the protocone is set far posteriorly on the tooth as well as far lingually, causing the trigon basin to be wide, unlike the condition in other pakicetid genera. The two species of *Pakicetus* differ in shape of the molar protocone: *P. inachus* resembles *Ichthyolestes* (slender, high protocone), while *P. attocki* is more similar to *Nalacetus* (low, robust protocone).

Pakicetus attocki (West, 1980)
(Fig. 2A, B; 3A, B; 4A–E, I–J)

Protocetus attocki West, 1980:515, fig. 1.5.
Protocetidae indet. (in part), West, 1980:516, fig. 1.6.
Pakicetus attocki (in part), Gingerich and Russell, 1981:242, fig. 5; 1990:14.
Ichthyolestes pinfoldi, Kumar and Sahni, 1985:166, fig. 7S–X.
Pakicetus sp., Thewissen and Hussain, 1993:fig. 1, 2; Thewissen, 1993:fig. 9 (in part); 1994:fig. 2 (in part).

Holotype.—H–GSP 1694, mandible with P_{3-4} (not

P_4–M_1 as stated in the type description), and alveoli or roots for several other teeth. The number for the holotype listed in figure 1.5 of West (1980) has transposed digits. The holotype is now lost.

Diagnosis.—Protocone of upper molars large and bulbous. Cristae strong, paracrista stronger than metacrista and giving rise to a wide trigon basin.

Type Locality.—H–GSP Locality 62, Kala Chitta Hills.

Age and Distribution.—Early and middle Eocene, redbeds of the lower Kuldana Formation and Subathu Formation, northern Pakistan and northwestern India.

Referred Specimens.—H–GSP Locality 62: H–GSP 18399 (fragment of P^x, probably P^2, preserving one root and a cast for a second root); H–GSP 18410 (M_x, probably M_2); H–GSP 18431 (fragment of P^x, probably P^1); H–GSP 18467 (premaxilla/maxilla fragment with partial alveolus for I^1, complete alveoli for I^2–C^1 and crown of I^3); H–GSP 18470 (maxilla with P^4–M^3 and alveoli for P^3); H–GSP 18483 (P^x fragment); H–GSP 18489 (left tympanic); H–GSP 18519 (C^1); H–GSP 18495 (fragments of dentary, including mandibular condyle and a fragment with alveoli for I_1–P_3); H–GSP 91014 (M^1); H–GSP 91030 (probable I^x); H–GSP 91031 (fragmentary M^x, probably M^2); and H–GSP 91034 (dentary with alveoli for I_{1-3}, C_1, P_1, crowns for dP_{2-4}, M_1, and a small, unerupted fragment of M_2. These teeth were misidentified by Thewissen and Hussain [1993], and dP_2 was sacrificed for stable isotope analysis); H–GSP 91035 (left tympanic with incus). Locality unclear but Ganda Kas Area: BMNH M–15806 (mandible with dP_3); H–GSP 535 (dentary with M_x fragment). East Babbian Gala, Subathu Formation: VPL/K 706.

Description.—There are three upper incisors (H–GSP 18467), the alveolus for I^2 is 15.5 mm long and 11.7 mm wide, and the part of the alveolus for the first incisor suggests that it was similar in size. The alveolus for I^3 is substantially smaller. The base of I^3 is preserved and it shows that the crown was low and tapers strongly. At its base, I^3 was 9.3 mm long and 6.3 mm wide. The incisors are not juxtaposed and they are arranged anteroposteriorly, not linguolabially. The alveolus for the canine is larger than that for the incisors, 14.5 mm – 12.0 mm, and is crossed by the suture of maxilla and premaxilla. The premaxilla also preserves the lateral edge of the nasal opening. The dorsal edge of the premaxilla is smooth and rounded above the alveoli of I^1 and half of I^2, indicating that the premaxilla formed the edge of the nasal opening here. Caudal to this, it is grooved for attachment of the nasal bones. It is possible that the nasal opening notched the nasal bones in the midline (these bones are not preserved) and its caudal extent is thus unclear, but the arrangement in H–GSP 18467 does indicate that the widest part of the nasal opening was probably over the anterior incisors.

The medial edge of the premaxilla is 19 mm wide (H–GSP 18467) lingual to the alveoli of I^{2-3}. This indicates that the snout was very narrow near its tip. Caudal to this is a groove for the nasopalatine duct and vomeronasal organ, opening on the palate through the palatine fissure (incisive fissure of Kellogg, 1928; anterior palatine foramen of Barnes, 1984). This foramen is 16.6 mm long.

An isolated single-rooted tooth may represent an upper incisor (H–GSP 91030). It is pointed and has a strongly convex labial side. Its lingual side is more or less flat and has a weak cingulum, strong crests extend to the base of the tooth from its tip. Its length is 10.8 mm and its width 5.4 mm, crown height is 12.5 mm.

C^1 (H–GSP 18519) has a stout crown with crenulated enamel, its lingual side is less convex than its labial side. Crown and root are somewhat curved. A weak crest extends down the anterior aspect of the tooth and a stronger crest extends down the posterior side. This latter crest divides into two parallel crests that extend to the enamel–dentine junction. Length of the canine (anteroposteriorly) is approximately 19 mm, and minimum crown height is 32 mm. The root is longer than wide and bears a longitudinal groove labially.

The presumed P^1 (H–GSP 18431) has a robust, high, straight crown with one cusp. The enamel is crenulated, and a crest ascends the paracone from cingulum to tip. The cingulum is complete lingually, but is lacking labially. The boundary between enamel and root flares occlusally in the center of the tooth, reflecting its yoke-like shape. It is single rooted, and the cross section of the root is ovoid, narrower anteriorly than posteriorly. Length at the base is approximately 12.5 mm, width is 9.6 mm. The crown is worn apically; it is approximately 23 mm high.

A presumed P^2 (H–GSP 18399) has a robust and high crown and is double rooted. There is a faint labial cingulum, and a somewhat stronger lingual cingulum. The tooth is yoke-shaped. A wear facet exposes dentine along the entire anterior edge of the tooth. The roots are close together; the shortest distance between them at the lowest point of crown–root junction is 3.3 mm. Crown width is 8.7 mm, crown height approximately 21 mm.

The maxilla posterior to P^2 is known from one well-preserved specimen (H–GSP 18470). P^3 has two roots, and was longer than P^4. P^4 has a single cusp, a high paracone, and a strong lingual bulge (but no protocone). It lacks styles and has three roots. The cingulum surrounding the lingual bulge is strong, and other cingula are weak.

M^1 (partly preserved as an epoxy endocast in H–GSP 18470) has a large paracone and a somewhat smaller, connate metacone. The protocone is lower than the labial cusps and set far lingually. The enamel of the central part of the tooth is worn off, but remains of dentine show that a low paracrista was present. Weak anterior and posterior notches separate the protocone from the labial cusps. Paracrista and metacrista are present; there is a weak labial cingulum, and no lingual cingulum. M^1 length is 14.8 mm and its width is 15.8 mm. An isolated upper molar (H–GSP 91014) lacks the central part of the tooth, but is similar to M^1 of H–GSP 18470 in other respects.

M^2 is much larger than M^1, but similar in shape (H–GSP 18470: length 18.7 mm, width 20.7 mm). The paracrista is stronger than the metacrista, and these crests are better preserved than on M^1 in H–GSP 18470. Weak anterior and posterior cingula are present on this tooth. M^2 is similar in width, but longer than M^3. The metacone of M^3 forms only a low bulge on the postparacrista, barely elevated above the crest. Paracrista and metacrista are present on all molars. Cingula are continuous labially, but

interrupted lingually. Length of M^3 is 15.6 mm, width 20.8 mm (H–GSP 18470). The basal outline of an upper molar is retained in H–GSP 91031, but enamel only remains on the protocone. It is similar to the protocone of H–GSP 18470.

The palate (H–GSP 18470) shows depressions between the lingual sides of all teeth from P^4 to M^3. These embrasure pits are perforated by vascular foramina and probably received the cusps of the lower teeth when the jaws were in occlusion. The midsagittal palatal suture is also preserved. Near the anterior root of P^3 the right half of the palate was 19 mm wide; near the protocone of M^3 it was 38 mm. A small palatine foramen occurs lingual to M^1. The palate reached caudal to M^3 and the teeth do not extend onto the zygomatic arch. On the face, the joint for the jugal reaches as far anterior as M^3. A tapering maxillary sinus is present over the molars and ends over P^4. The lateral wall of the nasal cavity is also preserved and the contact with the nasals is visible. The height of the maxilla is 45 mm dorsal to P^3. The maxilla is directed more or less medial at this point, indicating that the nasals add little to the height of the face. The width of the nasals can be estimated because the midsagittal plane is preserved at the palate. Projecting this plane dorsally implies that the right nasal was approximately 8 mm wide. This indicates that the nasal opening was well anterior to P^3, consistent with the morphology of the premaxilla. The infraorbital canal can be traced for its entire length, it opens on the face over P^3. The foramen is small, its greatest diameter is 6.6 mm.

The anterior part of the dentary (H–GSP 18495) has a convex inferior border and tapers (depth below P_2 is 27 mm, depth below I_3 is 21 mm). I_1 was small; its alveolus is approximately 5.2 mm, and is immediately adjacent to the contralateral I_1. There is no diastema between I_1 and I_2, and these two teeth were probably implanted mediolaterally, not anteroposteriorly. I_2 is much larger than I_1; the alveolus for I_2 is 13 mm long. I_3 is smaller again; its alveolus is 11 mm long. A diastema of 2.5 mm separates it from the canine alveolus, which is 17.5 mm long and 8 mm wide. P_1 was single rooted; its alveolus was approximately 13 mm long, and its root was straight. The diastema between P_1 and P_2 is 3.2 mm. Two alveoli with roots are present for P_2; their maximum length is 20.5 mm, and their width is 6.4 mm. The anterior edge of the alveolus for P_3 is 9.1 mm from P_2. The mandibular symphysis reaches just beyond the posterior root of P_2. The mandibular canal at the anterior root of P_3 is 10.8 mm high and 7.4 mm wide.

Overall, the shape of H–GSP 18495 matches that of the juvenile mandible (H–GSP 91034), although the latter is smaller. Alveoli for the incisors are poorly preserved, but dI_1 was medial to and smaller than dI_2. A germ for I_3 is preserved in the alveolus of dI_3; it has a pointed tip. The alveolus for dC_1 is smaller than that for P_1. Both are single rooted, and they are separated by a short diastema (3.3 mm). The crown of dP_2 is preserved; it has thin enamel, and is barely yoke-shaped. It bears a single cusp and is longer (12.9 mm) than high (10.3 mm). dP_3 is poorly preserved, but it, too, is double rooted and has a single triangular cusp. In contrast to dP_2, dP_3 has a posteriorly extended area that resembles the talonid, but it lacks a talonid basin. It is possible that a small hypoconid was present. Length of this tooth is 14.8 mm, and width approximately 4.6 mm. The tip of the protoconid was 9.5 mm above its base. Gingerich and Russell (1981) described a tooth in a mandible (BMNH M-15806) as a probable dP_3 of *P. attocki*. We concur with this identification.

The mandibular symphysis reaches below dP_2 (in H–GSP 91034). The mandibular foramen is preserved caudally, where it

is 5.8 mm high. The ascending ramus is steeply inclined unlike later archaeocetes, although its maximum height is only 45 mm.

dP_4 (H–GSP 91034) is long and narrow (length 20.7 mm, approximate width 5.3 mm). It lacks a concave anterior outline and lacks stylids on the anterior cingulid. The paraconid is large, well separated from the protoconid. It is nearly as high as the protoconid, and slightly shorter anteroposteriorly. It is directly anterior to the protoconid and a crest extends from the anterior cingulid to its tip and from there to the protoconid. The metaconid is a small cusp on the posterolingual flank of the protoconid. The talonid bears one cusp, somewhat smaller than the paraconid.

The lower molars (H–GSP 18410) have a large protoconid which dominates the trigonid. The paraconid (H–GSP 18410) and the metaconid (H–GSP 91034) are small, set on the side of the protoconid. The anterior cingulid is strong and concave anteriorly. Two crests ascend the trigonid from here. The first is on the lingual side and ends in the paraconid, the second is on the labial side and fades while ascending the protoconid (H–GSP 18410). The lingual cingulid is complete; there is a weak posterior cingulid and no labial cingulid. The talonid bears one cusp, the hypoconid, with a sharp cristid obliqua and a weak posthypocristid. A fragmentary and poorly mineralized trigonid of M_2 occurs in the dentary of H–GSP 91034.

Discussion.—*Pakicetus attocki* is the largest cetacean from the lower Kuldana Formation of the Kala Chitta Hills, and the taxon is morphologically distinct. The dentary of *P. attocki* is characteristic of the genus. Three referred specimens from H–GSP Locality 62 (H–GSP 18495, 91014, and 91034) resemble the type specimen (H–GSP 1694) in tapering anteriorly and in having a convex inferior side. In this respect they are unlike *Ichthyolestes*. Size of the diastemata are larger than in *Nalacetus*. In addition, dP_4 (H–GSP 91014 and 91034) differs from dP_4 of *Nalacetus* in the absence of an anterior re-entrant groove and from those of *Nalacetus* and *Ichthyolestes* in the longer overall shape with the large paraconid.

Lower molars are best referred to *Pakicetus* on the basis of their size (Fig. 1) and robustness (H–GSP 18410). Morphologically, they differ from *Ichthyolestes* in that the trigonid is shorter and usually lacks a lingual rib. The paraconid is smaller than in *Nalacetus*.

The upper incisors of *Pakicetus* are low and robust, unlike the high incisors described by Gingerich and Russell (1990), which probably represent *Ichthyolestes*. Lower and upper canine (H–GSP 18519) are distinguished on the basis of the greater curvature of the root in the latter. H–GSP 18467 is referred to *P. attocki* based on its robusticity and its poor match with anterior dentaries of *Ichthyolestes* and *Nalacetus*. H–GSP 91030 is an upper incisor of *P. attocki* referred on the basis of its robusticity, and its apparent good fit in premaxilla H–GSP 18467. It could also be a lower incisor. H–GSP 18519 is

an upper canine of *P. attocki* that fits the canine alveolus of H–GSP 18467 well. It bears a long wear facet on its anterior face, indicating that it occluded with a long tooth anterior to it. Given that I^3 is short, this tooth must be an upper canine.

Upper molars of *Pakicetus* are clearly different from those of other pakicetids. These teeth have a robust lingual protocone, wide trigon basin, and well-separated labial cusps. The maxilla of *P. attocki* indicates that there is a large size difference between M^1 and M^2 (H–GSP 18470), and that M^3 is wider than M^2, but shorter (similar to the holotype of *Ichthyolestes*). This size difference allows identification of isolated upper molars. The small size of H–GSP 91014 suggests that it is M^1, while the much larger H–GSP 91031 is probably M^2.

A single-rooted tooth (H–GSP 18431) is more robust than teeth referred to *Nalacetus* and *Ichthyolestes*. It has a high crown and is thus not an incisor, and its crown is straight, unlike the canine. Its root is too robust to fit any alveolus in the lower dentition (H–GSP 18495). It therefore probably represents P^1. The length/width ratio of H–GSP 18399 is smaller than in known lower premolars. Its roots are close together, unlike P^3, and it may represent P^2. Its robustness does not match any tooth of *Nalacetus* and *Ichthyolestes*. H–GSP 18483 is a small premolar fragment that resembles H–GSP 18399 in robustness.

West (1980) interpreted the type specimen of *Pakicetus attocki* as having an M_1 with one large triangular cusp, similar to the tooth that he identified as P_4, and different from his M_2. It is now clear that West's "M_1" is actually P_4, and that P_{2-4} are similar in morphology (double rooted, triangular in lateral view, single cusped), and very different from the molars (trigonid with three cusps, talonid with one). This has several implications for the interpretation of the type specimen. M_3 of this specimen is not erupted, indicating that the specimen is a juvenile. This explains the small size of the mandible (depth below C_1 is 20 mm, whereas it is 26 mm in H–GSP 18495). The mandibular symphysis in H–GSP 18495 reaches caudal to P_2. A problem that remains is that West (1980) observed a double-rooted tooth in the P_1 position (his P_2). All other known pakicetids have a single-rooted P_1. This discrepancy cannot be resolved without renewed study of the holotype.

Gingerich (1977) and Gingerich and Russell (1981) described a mandible with a deciduous premolar (BMNH M-15806) as *P. attocki*. Matrix adherent to this specimen indicates that it was found in the red conglomerates of the lower Kuldana Formation and was not necessarily associated with the marine vertebrates from the same locality (Gingerich, personal communication, 1995). West (1980) described a fragmentary lower molar and dentary from an unspecified locality near Ganda Kas in the Kala Chitta Hills (H–GSP 535). The specimen cannot be measured, but the trigonid (as figured by West) suggests that it most likely is *P. attocki*. Gingerich and Russell (1990) referred UM 65868, a fragmentary lower molar, from the Kala Chitta Hills to *Pakicetus attocki*. The specimen, which was recovered in the Kohat Limestone, was previously referred to *Gandakasia* by Gingerich (1977). It has a long trigonid, unlike pakicetids, and probably pertains to *Gandakasia*.

Two tympanics from the Kala Chitta Hills (H–GSP 18489 and 91035) are here referred to *P. attocki* on the basis of their similarity to the holotype of *Pakicetus inachus* and the realization that the latter species is very rare in the Ganda Kas area. A third cetacean tympanic (H–GSP 18391) differs morphologically from *Pakicetus*, and cannot yet be identified.

Kumar and Sahni (1985) referred a maxilla with two teeth from the Subathu Formation (VPL/K 706) to *Ichthyolestes pinfoldi*. Although these teeth are too damaged to be measured, direct comparison indicates that they are similar in size to *Pakicetus attocki*, and show the characteristic large protocone and separation of labial cusps of this species.

Pakicetus inachus Gingerich and Russell, 1981
(Fig. 6)

Ichthyolestes pinfoldi, West, 1980:516, fig. 2.1.
Pakicetus inachus Gingerich and Russell, 1981:238, fig. 2–4; Gingerich et al., 1983:404; Gingerich and Russell, 1990 (in part):3, fig. 1–5, 6A–H, and 6M–O.

Holotype.—UM–GSP 84, braincase, described by Gingerich and Russell (1981) and Gingerich et al. (1983). Since the return of this specimen to its repository, the specimen has suffered considerably (loss of both zygomatic arches, damage to occipital condyle).

Age and Distribution.—Early Eocene, redbeds of the lower Kuldana Formation. Locality Chorlakki, Kohat District, Northwest Frontier Province and H–GSP Locality 62 (Kala Chitta Hills), Kala Chitta Hills, Punjab, Pakistan.

Revised Diagnosis.—Protocone of upper molars slender and low. Cristae on upper molars weak, metacrista commonly absent.

Referred Specimens.—Chorlakki: UM–GSP 81

(dentary with P_{2-4}); UM–GSP 82 (M_x); UM–GSP 83 (M^1); UM–GSP 85 (M^1); UM–GSP 113 (trigonid); UM–GSP 134 (M^2, labial fragment); UM–GSP 147 (P^4 fragment); UM–GSP 751 (P^4 fragment); UM–GSP 1672 (M^1). H–GSP Loc. 62: H–GSP 1981b (M^2, also listed as H–GSP 1981 by West, 1980:516). Probable *P. inachus* from Chorlakki: UM–GSP 108, 136, 749, 750, 1401, 1409, 1450, 1509, 1653, 1722, 1937, and 1938 (described by Gingerich and Russell, 1990).

Description.—The description of the holotype skull by Gingerich and Russell (1981) and Gingerich et al. (1983) focussed on the ear region. Here, we present additional details of the basicranium and orbitotemporal fossa and add stereo photographs (Fig. 6).

The base of the orbitotemporal fossa is distorted, but the proportions of the interorbital region can still be studied. Most of the sagittal crest is preserved, and in the interorbital region it was as high dorsoventrally as the remainder of the braincase (both approximately 20 mm). The pterygoid processes are considerably deformed and it is unclear which bone forms them. In this area they are more than 35 mm high (dorsoventrally). They taper caudally and end anterior to the middle ear. Their caudal-most part flares laterally and ends anterolateral to the bony part of the auditory tube. This part of the pterygoid processes is apparently formed mostly by the alisphenoid. It bears a low lateral process (possibly the hamulus), and shallow grooves extend craniocaudal on it.

The orbitotemporal fossa bears one large foramen near the root of the pterygoid process. A deep groove extends craniocaudally from this foramen, and on the left side a smaller shallow groove extends inferiorly. Its position suggests that this foramen is the sphenorbital fissure. This part of the braincase was extremely long in life, as there is no trace of the optic foramen for the 15 mm cranial to the sphenorbital fissure. The foramen rotundum is also lacking. The oval foramen is present just medial to the posteriormost part of the pterygoid process.

Lateral to the oval foramen is a flat, slightly elevated area on the squamosal for articulation with the ectotympanic (bullar process of squamosal as described by Gingerich and Russell, 1981). The ectotympanic is preserved on the right side of the specimen. It has a long contact with the basioccipital that was interpreted by Gingerich and Russell (1981:240) as an "articulation." However, the left side of the specimen (which lacks the tympanic) shows no facet on the basioccipital, and there is no evidence for it on isolated ectotympanics of *P. attocki* (H–GSP 18489 and 91035). We interpret the medial contact in the holotype as the result of crushing. This is confirmed by the absence on the lateral side of the tympanic of such structures as the opening for the external auditory meatus, which was apparently crushed and is now covered by the ectotympanic. The basioccipital bears a pair of low elevations medial to the middle ear, probably attachment sites for the neck musculature. There is no falcate process. The hypoglossal foramen (for cranial nerve XII) is immediately medial to the jugular foramen (for cranial nerves IX–XI and internal jugular vein); the distance between the two is 1.3 mm. The condylar canal (for an emissary vein) opens caudal to the jugular foramen, caudolateral to the hypoglossal canal. The condylar foramen is immediately anterior to the occipital condyle. The paroccipital process extends caudolateral from the area immediately caudal to the jugular foramen. It forms a ridge that terminates in a plane caudal to the occipital condyles. Its medial part is grooved anteriorly by the canal for the facial nerve.

Discussion.—The type specimen of *P. inachus* is a basicranium from Chorlakki that cannot be compared directly with any other lower Kuldana cetacean. Gingerich and Russell (1981, 1990) and Gingerich et al. (1983) assumed that only one cetacean species, *Pakicetus inachus*, occurred at the Chorlakki locality and referred all cetacean material from this site to this species. One of the referred specimens was a mandible with three premolars (UM–GSP 83) that formed (by necessity) the sole basis for comparison with *P. attocki*. Based (by necessity) on one specimen of each of the species, Gingerich and Russell (1981) noted one diagnostic difference between the species of *Pakicetus*: the absence of serrations on the anterior and posterior crests of the premolars. As suggested by Gingerich and Russell (1990:14), it is unclear whether this difference merits specific distinction. However, new dental material confirms that the two species are morphologically distinct.

Isolated upper cheek teeth of *P. inachus* can be identified on the basis of comparisons with a maxilla of *P. attocki*. Based on isolated molars, Gingerich and Russell (1990) proposed that M^2 was smaller than M^1 in *Pakicetus inachus*, but the size relation is probably the reverse, given the arrangement in *P. attocki*. Upper molars from Chorlakki referable to *P. inachus* include two small M^1s (UM–GSP 83 and 1672) and an M^3 (UM–GSP 85). These molars resemble those of *Ichthyolestes* in the size and shape of the protocone, but they resemble *P. attocki* in size and in the posterior position of this cusp. A labial tooth fragment (UM–GSP 134) has slender labial cusps and is probably also referable to *P. inachus*; it is larger than the M^1s and is therefore probably M^2.

A single upper molar from H–GSP Locality 62 is here referred to *P. inachus* (H–GSP 1981b). This tooth is longer than any upper molar of *P. attocki*, and matches the Chorlakki M^2 (UM–GSP 134) in size. It has slender labial cusps and a slender protocone, with weakly developed crests, all similarities to the topotype material of *P. inachus*. West (1980) stated that this tooth had not erupted and was prepared free from the maxilla. He referred it to *Ichthyolestes pinfoldi*, but the specimen is longer (approximately 1.5 times) and wider (approximately 1.3 times) than the holotype. It resembles *Ichthyolestes* and *P. inachus* (but not *P. attocki*) in the shape of the protocone.
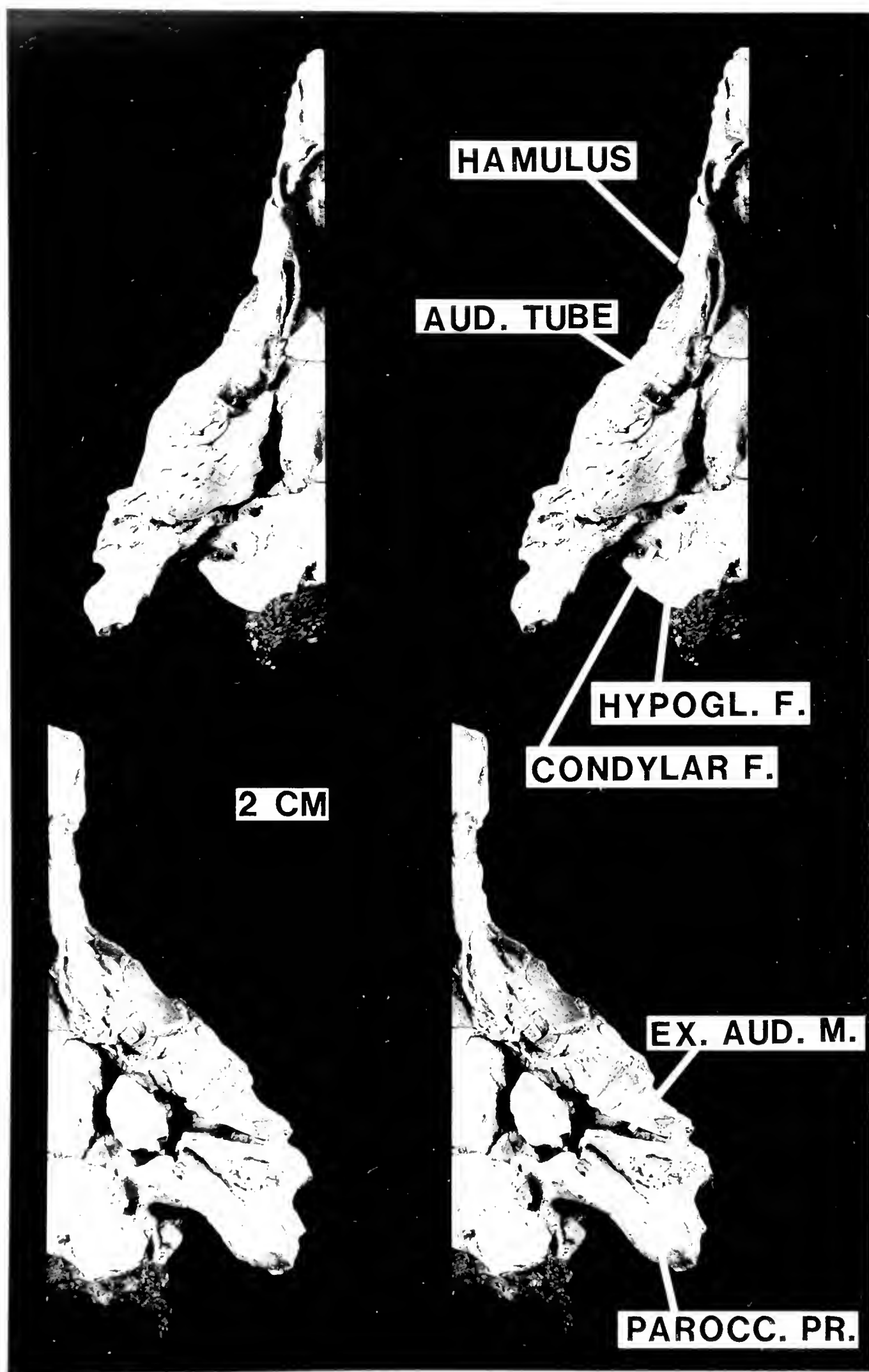
Fig. 6.—Right and left sides of basicranium of holotype of *Pakicetus inachus* (UM-GSP 84), stereopairs. Many auditory structures were described in detail by Gingerich and Russell (1981) and Gingerich et al. (1993). Other structures that are visible include hypoglossal foramen (HYPOGL. F.), condylar foramen (CONDYLAR F.), paroccipital process (PAROCC. PR.), presumed pterygoid hamulus, bony groove for the auditory tube (AUD. TUBE), and external auditory meatus (EX. AUD. M.).

CONCLUSIONS

In 1984, Barnes summarized the older literature on cetacean evolution and identified a "unique suite of derived characters" (p. 139) for the order. In the years since then, understanding of cetacean evolution has greatly increased. As more intermediate forms are discovered, it is becoming clear that most of Barnes' features do not characterize the order. This does not distract from the importance of Barnes' summary, it is only to be expected that new fossils fill gaps in the fossil record. Pakicetids are crucial to our understanding of the origin of cetaceans because they are the most basal branch on the cetacean cladogram. Here, we briefly evaluate Barnes' characters.

Gingerich and Russell (1981) described a braincase for *Pakicetus inachus* that lacks two of Barnes' characters (large falcate processes; peribullar and pterygoid sinuses). Material described in this paper and by Thewissen and Hussain (1993) shows that pakicetids lack the derived state for two more characters (anterior palatine foramina absent; large mandibular foramen). The presence of a large, horizontal supraorbital process cannot be studied in pakicetids, but this process is absent in *Ambulocetus* (Thewissen et al., 1996) and it therefore cannot be used to characterize cetaceans. The hypoglossal foramen is located at the apex of (or within) the jugular notch in many cetaceans, but a similar condition exists in several ungulates (Thewissen et al., 1996). The scapula remains unknown in the most primitive (pakicetid and ambulocetid) cetaceans, so the presence of the supraspinous fossa and its processes cannot be verified for the most critical clades.

Development of the involucrum of the tympanic in primitive cetaceans is well known. This is the only character listed by Barnes (1984) for which the distribution among cetaceans is well known and that can be used to characterize the order.

A full review of cetacean synapomorphies cannot be undertaken because many important clades are very incompletely known, but a heuristic discussion of the subject was published by Thewissen (1994). Pakicetids (*Ichthyolestes*, *Nalacetus*, and *Pakicetus*) form a distinct morphological cluster that can be defined using a combination of primitive and derived features. It is likely that these early cetaceans form a monophyletic group, but this cannot be demonstrated at present because of low sample sizes of dental elements for these genera and because few nondental elements are known for more than one genus.

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MIDDLE EOCENE STRATIGRAPHY AND MARINE MAMMALS (MAMMALIA: CETACEA AND SIRENIA) OF THE SULAIMAN RANGE, PAKISTAN

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ABSTRACT

Field work in the Sulaiman Range of southwestern Punjab has yielded four middle Eocene vertebrate faunas with marine mammals, principally archaeocete Cetacea. These are intermediate in age and bridge the temporal and morphological gap between two continental early Eocene faunas with amphibious archaeocetes in Kohat and northern Punjab (Pakistan), and later marine middle Eocene faunas with aquatic archaeocetes and sirenians in Kutch (India) and in Mokattam and Fayum (Egypt). The six Pakistan faunas are correlated to the geological time scale using global sea-level sequence stratigraphy, with planktonic foraminiferal and nannoplankton control (magnetization is weak where this has been sampled, with the present-day field predominating and little or no remanent Eocene primary magnetization). The two oldest faunas come from Kohat and northern Punjab: 1) the *Pakicetus* fluvial fauna comes from the lower Kuldana Formation, which is latest Ypresian in age (about 49.0 to 49.5 million years before present on the Haq et al. time scale); and 2) the *Ambulocetus* transitional-marine fauna comes from the upper Kuldana Formation, which is earliest Lutetian in age (about 49.0 to 48.0 Ma). Four succeeding faunas come from the Sulaiman Range: 3) the

Habib Rahi Formation deep-shelf marine fauna comes from platy limestones and is early Lutetian in age (about 48.0 to 46.5 Ma); 4) the lower Domanda Formation *Rodhocetus–Takracetus* middle-shelf marine fauna comes from green clays and limestones and is early middle Lutetian in age (about 46.5 to 46.0 Ma); 5) the middle Domanda Formation *Gaviacetus–Remingtonocetus–Dalanistes* shallow-shelf marine fauna comes from brown clays and is middle Lutetian in age (about 46.0 to 45.5 Ma); and 6) the middle Drazinda Formation *Babiacetus–Protosiren* middle-shelf marine fauna comes from green clays and is late middle Lutetian in age (about 43.5 Ma). The Drazinda Formation fauna is evidently younger than the long-known Egyptian *Protocetus–Protosiren* fauna of Gebel Mokattam (ca. 45.0 Ma), and the Indian *Indocetus–Remingtonocetus* fauna from Kutch probably lies in the interval spanned by these two (ca. 45.0 to 43.5 Ma). The six Pakistan faunas document successive stages of cetacean evolution through six million years of early and middle Eocene time in eastern Tethys that involved changes first in the dentition for feeding on fish, then in the basicranium and dentaries for hearing in water, and finally in the pelvic girdle and hind limbs for efficient tail-powered swimming.

INTRODUCTION

The first mammalian remains from Eocene strata of the Sulaiman Range of Pakistan were reported by Pilgrim (1940). Pilgrim described three specimens. The first was a maxilla that he identified as anthracotheroid, and the other two were a partial maxilla lacking teeth and a "bear-like" partial right pelvic bone or innominate, both identified as mesonychid creodont. These came from "blue-grey

shales weathering olive-green of the lower Khirthar" at Safed Toba, three to five miles south of Toba Kund, south of Kaha Nala (Fig. 1). This "lower Khirthar" is the "lower Chocolate Clays" of Eames (1952a, 1952b), or, in modern terminology, the Domanda Formation of Hemphill and Kidwai (1973) and Shah (1977, 1991). In Pilgrim's time, the Khirthar stage of Indo–Pakistan was known to
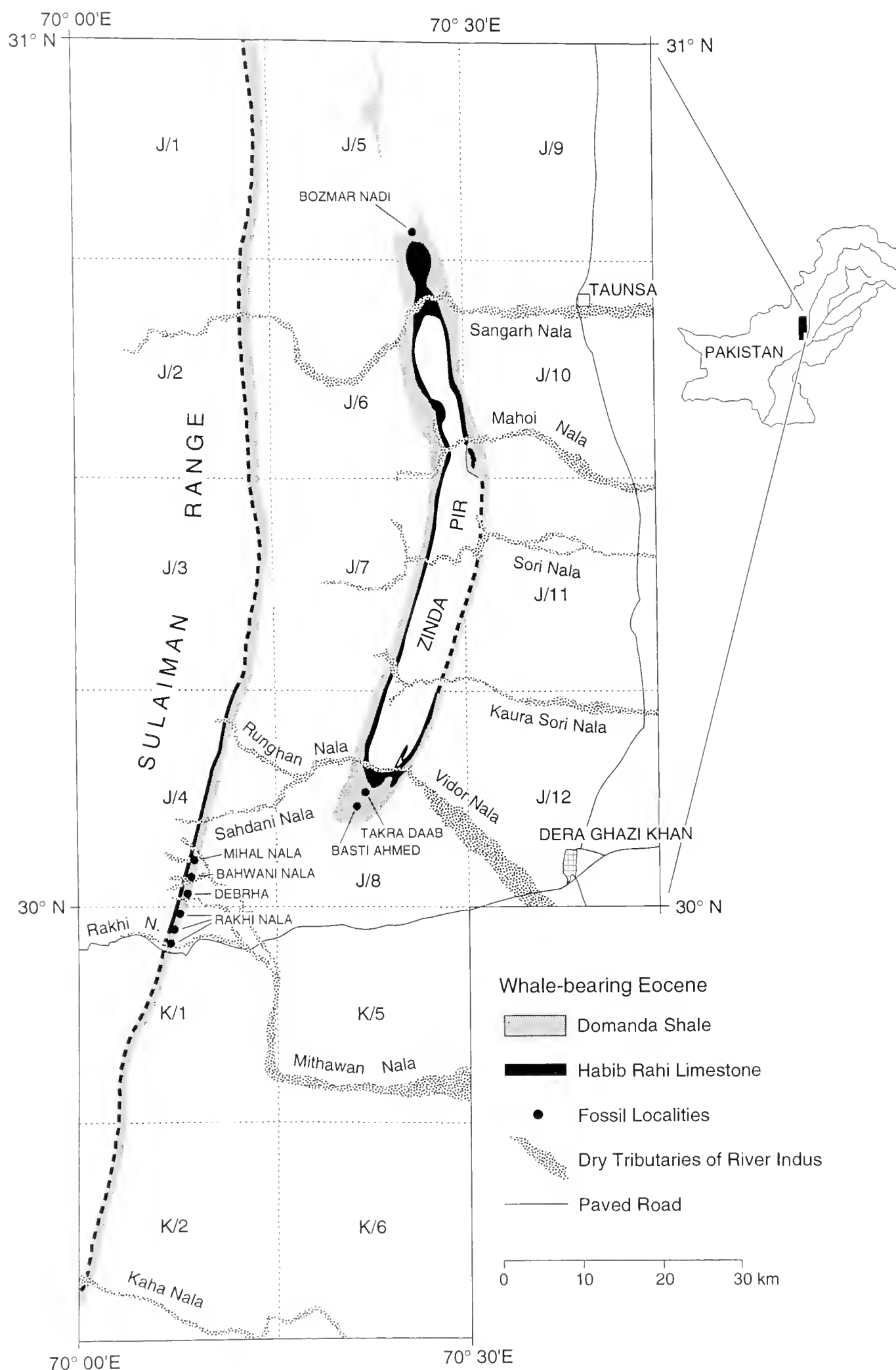
Fig. 1.—Map of Sulaiman Range and Zinda Pir antielinorium located on the west side of the Indus River in the southwest corner of Punjab, central Pakistan (inset). Northern fossil-bearing localities of Bozmar Nadi and Satta with specimens described by Gingerich et al. (1993, 1994, 1995b) are shown in relation to southern fossil-bearing localities of Takra Daab, Basti Ahmed, Debrha, Bahwani Nala, and Rakhi Nala with specimens described by Gingerich et al. (1993, 1995a). Stratigraphie sections shown in Figure 3 were measured on the north and south sides of the Rakhi Nala stream bed (southernmost Rakhi Nala locality shown here) and in nearby tributaries of Barghan Nala, the next drainage north of Rakhi Nala stream bed (middle Rakhi Nala locality shown here). Lithologies and thicknesses of middle Eocene formations studied here are very uniform over the entire map area, and the sections in Figure 3 are generally representative of sections studied throughout the field area.

CARNFORTH 109.

YEALAND CONYERS,
CARNFORTH,
LANCS.

28th February, 1956.

Dear Dr. Hopwood,

T.G.B.Davies tells me you would like more information regarding the Eocene vertebrates from W. Pakistan; I will try to call on you when next I am in London. Meantime, they are all from the same horizon, viz., the Lower Chharat of the Attock District in the north (Lammidhan and Chharat localities) and the Lower Chocolate Clays of Dera Ghazi Kahn District (Rakhi Gaj and Safaed Tobah). Eames states that this bed is the lowest bed of the Middle Eocene (Khirthar) and his full succession is given in Fig.3 of his paper, Q.J.G.S. vol.cvii,Pt.2,p.189,1952.

This formation marks a fresh water interlude in the marine Eocene: The Kohat Saline Series belongs to the "Platey Limestones"; the associated dolomitic limestones contain abundant fish remains throughout the region. The Lower Chocolate Clays overlie these beds and it is these beds which have yielded the vertebrate fossils. That they are definitely fresh-water deposits is indicated by the occurrence in limestone bands in them of <u>Planorbis</u> and other fresh-water shells, <u>Chara</u> spores and other plant remains. These beds pass upwards into richly fossiliferous foraminiferal shales and limestones which are definitely marine and Middle Eocene in age. Despite this profound alteration in the conditions of deposition, the succession is entirely regular over hundreds of miles of almost continuous outcrop. Only in our oil-field cores is there a suggestion of unconformity - in one or two wells we have obtained what looks like a basal conglomerate at the

2

base of the Lower Chharat beds.

The cranium was obtained from the Lower Chocolate Clays in the Rakhi Nullah valley, a short distance east of Rakhi Gaj (I believe my label says 3/4 miles E, but this was from our camp site - Rakhi Gaj of Eames's map (idem, Fig.2,p.161) is 1½ miles west of the Khirthar outcrop); the actual locality is 29°57'N,70°7'30"E.

I do not remember whether the snout came from the same locality, or from Safaed Tobah; if the latter, the locality is 29°27'N,69°57'E.

These beds are beautifully exposed over literally hundreds of miles in easily accessible country and very rich collections could be made from them. The fossils are sometimes coated with gypsum and ochre and are then easily seen in the red or chocolate clays.

Let me know if there is anything more that I can do. I am very glad they are proving of interest.

With kind regards,

Yours sincerely,

A. S. Pinfold.

Dr.A. Tyndale Hopwood,
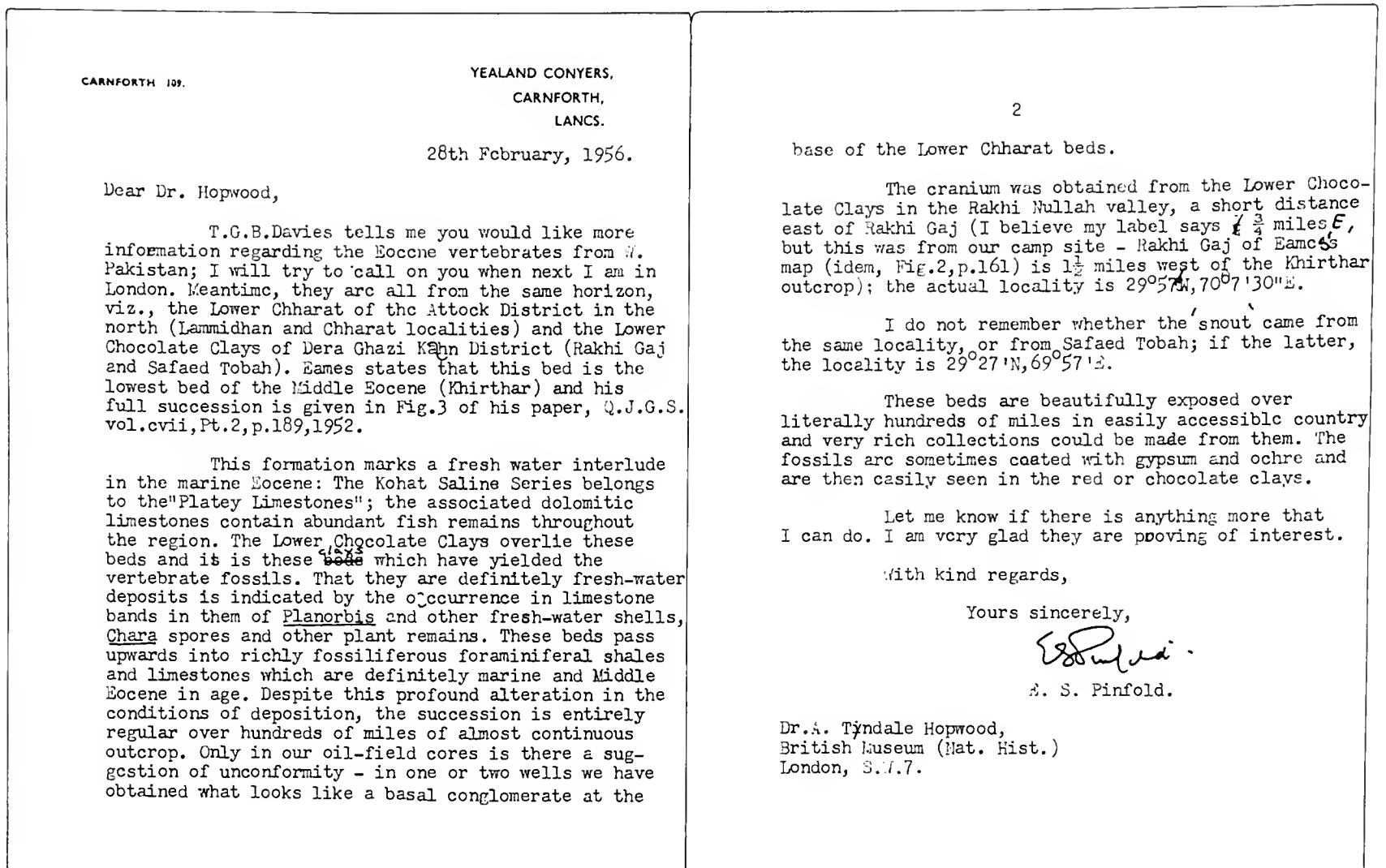British Museum (Nat. Hist.)
London, S.W.7.

Fig. 2.—Letter from E. S. Pinfold to A. Tyndale Hopwood, dated February 28, 1956, describing the promise of Eocene fossil vertebrate localities in the Domanda Formation or "Lower Chocolate Clays" of the Sulaiman Range of Pakistan. The cranium mentioned by Pinfold is M50719 in the Natural History Museum, London, United Kingdom, which is a partial cranium of *Dalanistes ahmedi* from the north side of Rakhi Nala east of Rakhi Gaj (locality shown in Figure 5). Safed Tobah, south of Kaha Nala on the map in Figure 1, is the source of the "mesonychid" maxilla described by Pilgrim (1940).

be an eastern-Tethys equivalent of the Lutetian stage of Europe, and the lower Khirthar was (and is) understood to be early middle Eocene in age.

Pilgrim (1940) also described land mammals from what is now the Kuldana Formation at Lammidhan in the Kala Chitta Range of northern Punjab. Broader exploration of the Kuldana Formation in the Kala Chitta Range was organized by Dehm and Oettingen-Spielberg (1958), who added two named "mesonychids," *Gandakasia potens* and *Ichthyolestes pinfoldi*, to the Kuldana Eocene fauna. In 1972, one of us (P.D.G.) visited Kuldana localities in the Kala Chitta Range and examined Kuldana and other Pakistan specimens at the British Museum (Natural History) in London. Accompanying specimens in a drawer in the British Museum was a letter from the geologist E. S. Pinfold to A. Tyndall Hopwood. The letter (reproduced in Fig. 2) mentions Lammidhan and Chharat in northern Punjab and Rakhi Gaj and Safed Tobah (or Toba) in the Sulaiman Range, and, citing Eames, implies that the lower Chocolate Clays are "definitely fresh-water,"

and states that these are "beautifully exposed over literally hundreds of miles in easily accessible country" where "very rich collections could be made."

The Lammidhan and Chharat localities were examined in more detail in 1975, when discovery of a "*Gandakasia*" tooth led to the suggestion that this "mesonychid" might be an archaeocete (Gingerich, 1977). At this time a team from Howard University (S. T. Hussain), Utrecht (H. de Bruijn), and the Milwaukee Public Museum (R. M. West) began to prospect the Kala Chitta Eocene intensively (Hussain et al., 1978; West, 1980), and a cooperative Geological Survey of Pakistan–University of Michigan (GSP–UM) research project was organized by P. D. Gingerich and D. E. Russell of the Muséum National d'Histoire Naturelle (Paris) to follow up on Pinfold's letter with exploration of the lower Chocolate Clays and other formations in other parts of Pakistan having the potential to yield land mammals.

In the field in 1977 it quickly became clear, contrary to the implication of Pinfold's letter, that the

lower Chocolate Clays (now Domanda Formation) are predominantly or entirely marine, having been deposited in the Tethys Sea on the passively-subsiding northwestern margin of Eocene Indo–Pakistan before uplift of the Himalayas. Fragmentary cranial and postcranial remains of archaeocete cetaceans were found in 1977, and Pilgrim's edentulous "mesonychid" maxilla from Safed Tobah was reinterpreted as representing, possibly, an archaeocete rather than a land mammal (Gingerich et al., 1979). Several massive sacra and innominates with large acetabula found in 1977 were facetiously dubbed "walking whales" in the field, but such whales were then unknown and the specimens were consequently considered more likely to represent moeritheriid or other amphibious land mammals carried into the sea (as Sahni and Mishra, 1975, had interpreted a sacrum from Kutch). Subsequent study has shown that all of these are archaeocetes, as are Pilgrim's Safed Tobah innominate and "anthracotheroid" maxilla and Sahni and Mishra's sacrum. Although disappointing for land mammals, the Eocene of Pakistan showed promise for investigating the early evolution of whales.

Interest in archaeocetes was rekindled by three developments in the 1960s and 1970s. First, Van Valen (1966, 1968) combined the results of comparative immunological study of myoglobins showing Cetacea to be the sister group of Artiodactyla (Boyden and Gemeroy, 1950) with his own understanding of early Cenozoic condylarthran mammals and proposed that Mesonychidae (or later, Mesonychia) are the group from which cetaceans evolved. Second, an important new archaeocete fauna was found and described from the marine middle Eocene of Kutch in India by Tandon (1971, 1976), Sahni and Mishra (1972, 1975), Satsangi and Mukhopadhyay (1975), Trivedy and Satsangi (1984), and Kumar and Sahni (1986). Finally, the cranium of a new and very primitive archaeocete, *Pakicetus inachus*, was found in fluvial deposits now known to be early Eocene in age at Chorlakki in Kohat District in the North-West Frontier Province of Pakistan (Gingerich and Russell, 1981; Gingerich et al., 1983). All of these discoveries served to focus attention on the early-to-middle Eocene as the time of origin, and eastern Tethys as the place of diversification, of the earliest Cetacea.

In 1981 a GSP-UM team including Neil Wells, Hassan Shaheed, David Bardack, and William Ryan returned to the Sulaiman Range to look for archaeocetes and other marine vertebrates. There, in addition to a substantial fauna of fishes, they found:

1) the skull included in *Indocetus* by Gingerich et al. (1993; now identified as *Rodhocetus*), 2) well-preserved dentaries described and named *Rodhocetus* by Gingerich et al. (1994), and 3) a partial skull of *Remingtonocetus* cf. *R. harudiensis* described by Gingerich et al. (1995a; identifications and re-identifications are explained in this paper). These specimens all came from the Domanda Formation. In addition, the GSP–UM team found a partially articulated skull and skeleton of a new archaeocete in the underlying Habib Rahi Formation (Gingerich, 1991), which Rahman and Dunkle (1966) had reported as yielding well-preserved marine fishes. Localities are described in Wells (1984) and in Gingerich et al. (1993, 1995a; see Fig. 1 here). The 1981 expedition proved that well-preserved archaeocetes can be found in the Domanda and other Eocene formations of the Sulaiman Range.

Further expeditions were organized in 1992 and 1994 to follow up on the 1977 and 1981 discoveries. Field work in 1992 was concentrated at the northern plunge of the Zinda Pir anticlinorium, particularly in the Domanda Formation of Bozmar Nadi (Fig. 1), and in the Drazinda Formation near Satta (north of Sangarh Nala, north of an area prospected by West et al., 1991; see also Case and West, 1991, and Nolf, 1991). Field work in 1994 was concentrated at the southern plunge of the Zinda Pir anticlinorium, particularly in the Domanda Formation of Takra Daab (Fig. 1). The 1994 field work yielded some ten cetacean skulls or partial skulls, including several with good associated postcranial remains. These show, when studied together with the Pilgrim–Pinfold specimens and our 1977, 1981, and 1992 collections, that there is considerable morphological and taxonomic diversity in early middle Eocene archaeocetes—much greater diversity than is known in late middle and late Eocene archaeocetes found in Egyptian Tethys or elsewhere. Diversity and its temporal succession are important for understanding the early evolution of whales. Six successive archaeocete faunas are now known from Pakistan, substantially improving our understanding of the timing and adaptive diversification of earliest Cetacea.

This paper combines results of Gingerich et al. (1995a, 1995b), with those of Sahni and Mishra (1975), Gingerich et al. (1983, 1993, 1994), Thewissen (1993), and Thewissen et al. (1994), using a stratigraphic framework to investigate the evolutionary chronology of cetacean evolution in eastern Tethys. Possible cetaceans from the early-to-middle

Eocene of Kashmir (Gingerich and Russell, 1994) are not considered here because of ambiguities concerning their age and identification.

Institutional acronyms used in text are: CGM, Cairo Geological Museum, Cairo, Egypt; GSI, Geological Survey of India, Calcutta, India; GSP–UM, Geological Survey of Pakistan–University of Michigan collection, Islamabad, Pakistan; H–GSP, How-ard University–Geological Survey of Pakistan collection, Islamabad, Pakistan; LUVP, Lucknow University vertebrate paleontology collection, Lucknow, India; NHML, Natural History Museum, London, United Kingdom; VPL/K, Kumar collection, Vertebrate Paleontology Laboratory, Panjab University, Chandigarh, India; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

EOCENE STRATIGRAPHY

Archaeocetes are known from three principal areas in Pakistan: the Kala Chitta Range in northern Punjab, the Kohat District in the North-West Frontier Province, and the Sulaiman Range in western Punjab. Extensive study of the micropaleontological stratigraphy and sea-level stratigraphy from various parts of the western Indo–Pakistan subcontinent has provided a means to correlate the archaeocete-bearing deposits from all three areas to the geological time scale.

KALA CHITTA RANGE AND KOHAT DISTRICT

The geology of Eocene deposits in the Kala Chitta Range of northern Punjab, whence Pilgrim (1940) and Dehm and Oettingen-Spielberg (1958) described Eocene land mammals, was studied by Cotter (1933). These Eocene deposits extend north and east into Hazara (Latif, 1970), and westward across the Indus River into Kohat District in North-West Frontier Province (Eames, 1952a, 1952b; Meissner et al., 1975). The principal land-mammal-bearing unit is the lower Kuldana Formation (or Mami Khel Formation), which is red mudstone with thin beds of calcarenite representing reworked soil nodules (Wells, 1983, 1984). These calcarenites sometimes preserve reasonably complete skulls (e.g., the holotype of *Pakicetus inachus*) and even skeletons of mammals (e.g., the *Diacodexis pakistanensis* skeletons described by Thewissen et al., 1983), and the entire vertebrate fauna is continental with no marine taxa (Pilgrim, 1940; Dehm and Oettingen-Spielberg, 1958; Buffetaut, 1978; Hussain et al., 1978; Russell and Gingerich, 1980, 1981, 1987; West, 1980; de Bruijn et al., 1982; Hartenberger, 1982; Gingerich et al., 1983; Thewissen et al., 1983, 1987; de Broin, 1987; Gayet, 1987; Rage, 1987; Roe, 1991), except, possibly, archaeocetes like *Ichthy-olestes* and *Pakicetus*. Lower Kuldana red beds are interpreted as clastic low-stand wedge deposits that grade laterally and offshore into Bahadur Khel salt and Jatta gypsum in Kohat District, which are equivalent to Baska gypsum farther south along strike in the Sulaiman Range.

The upper Kuldana Formation is a thin unit of green shales with oyster beds and other indications of shallow marine deposition (Wells, 1984). Mammals are rare elements of the fauna, and these generally represent more amphibious groups like anthracobunids (Wells and Gingerich, 1983) and *Ambulocetus* (Thewissen et al., 1994). The upper Kuldana shales are overlain by nummulite-rich marine Kohat Limestone, which has not yet been found to yield mammalian fossils. The Kohat Limestone was probably deposited during the TA3.2 sea-level highstand, correlative with Habib Rahi deposition in the Sulaiman Range farther to the south (see below).

SULAIMAN RANGE

In 1994 we spent ten days in the Sulaiman Range studying the classic Eocene stratigraphic section exposed in Rakhi Nala near Rakhi Gaj police post. Five formations were examined: 1) the 122 m-thick Baska Shale, "shales with alabaster," or Baska Formation, consisting of interbedded green shales and thin limestones with 10 m of bedded to massive gypsum near the top (Fig. 3, 4); 2) the 43 m-thick Habib Rahi Formation or "platy limestone" consisting of platy limestone and marl alternating with green shale, with limestones 10 cm thick at the base of the formation thinning and becoming more distantly spaced upward in the section (Fig. 3, 5); 3) the 303 m-thick Domanda Formation or "lower chocolate clays" consisting of green clay shale (sometimes fissile paper shales) at the base, brown clay shales in the middle, and brown shales with a lignite near the top (Fig. 3, 5); 4) the 12 m-thick Pir Koh Limestone or "white marl band" (Fig. 3, 6, 7); and 5) the 331 m-thick Drazinda Formation or "upper chocolate clays" consisting of green clay shales with some *Discocyclina*-rich limestones in the lower part and brown to red shales in the upper part (Fig. 6). The upper contact of the Drazinda For-
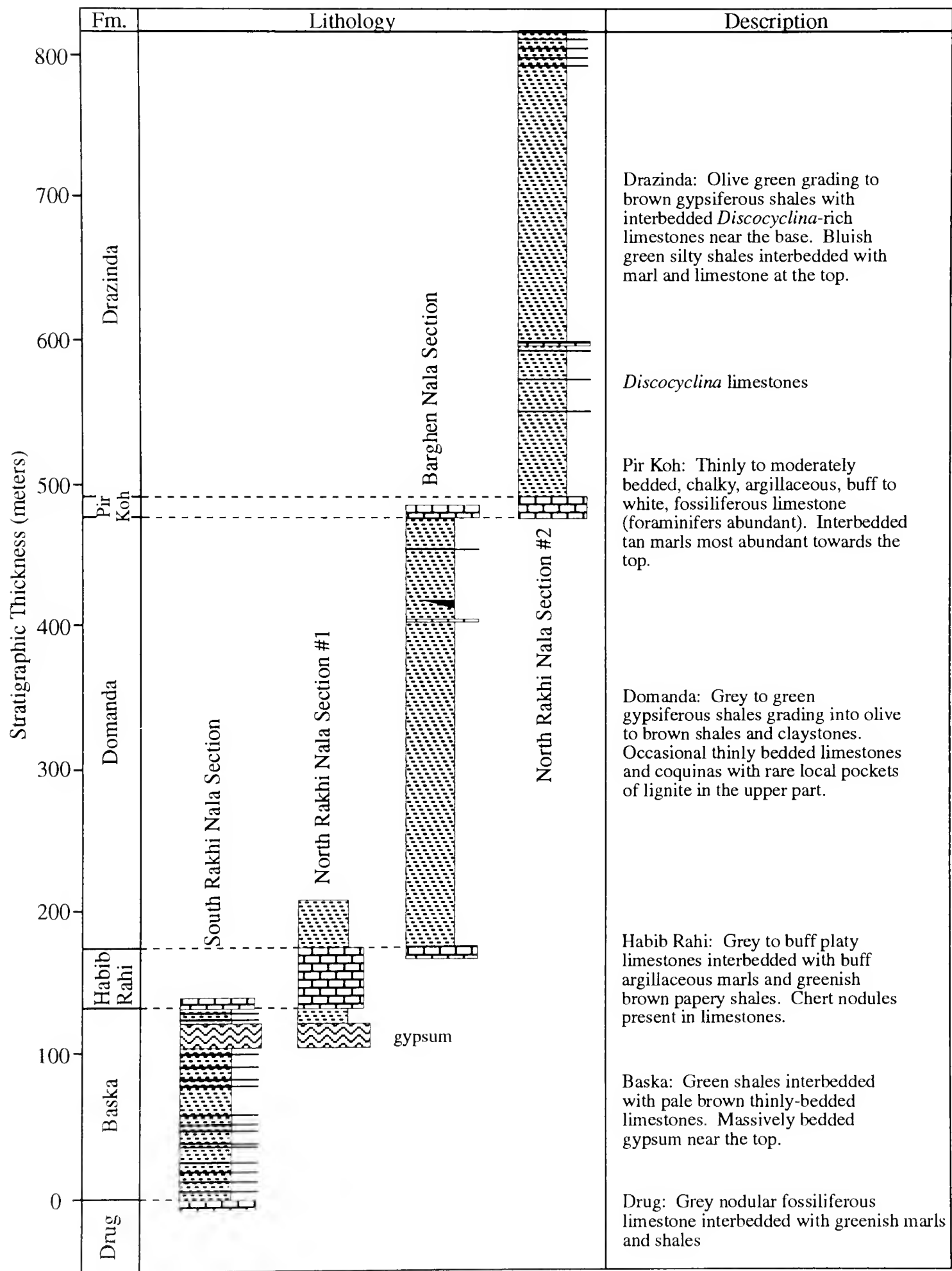
Rakhi Nala Stratigraphic Sections

Fm.	Lithology	Description

Drazinda: Olive green grading to brown gypsiferous shales with interbedded *Discocyclina*-rich limestones near the base. Bluish green silty shales interbedded with marl and limestone at the top.

Discocyclina limestones

Pir Koh: Thinly to moderately bedded, chalky, argillaceous, buff to white, fossiliferous limestone (foraminifers abundant). Interbedded tan marls most abundant towards the top.

Domanda: Grey to green gypsiferous shales grading into olive to brown shales and claystones. Occasional thinly bedded limestones and coquinas with rare local pockets of lignite in the upper part.

Habib Rahi: Grey to buff platy limestones interbedded with buff argillaceous marls and greenish brown papery shales. Chert nodules present in limestones.

Baska: Green shales interbedded with pale brown thinly-bedded limestones. Massively bedded gypsum near the top.

Drug: Grey nodular fossiliferous limestone interbedded with greenish marls and shales

Fig. 3.—Diagrammatic summary of stratigraphic sections of lower and middle Eocene formations measured by the authors in and just north of Rakhi Nala in November 1994. Formational thicknesses are listed Table 1. Baska Formation is best exposed on the south side of Rakhi Nala (Fig. 4). Habib Rahi Formation is best exposed on the north side of Rakhi Nala (Fig. 5). Domanda Formation is best exposed in Barghen Nala just north of Rakhi Nala proper (Fig. 6). Pir Koh Formation (Fig. 7) and Drazinda Formation are best exposed on the north side of Rakhi Nala, where they are overlain disconformably by the continental Miocene Chitarwata Formation.

Fig. 4.—Photograph of about 5 m-thick, massive, fine-grained Baska gypsum in the Baska Formation (or Baska Member of the Ghazij Formation), as exposed on the south side of Rakhi Nala (29°56′58″N latitude, 70°6′56″E longitude). View is to the south. Note that the top of the Baska gypsum (white slope dipping toward camera) has an undulating surface (arrows), suggesting subaerial exposure and weathering before deposition of overlying green shale passage beds. This gypsum, like Bahadur Khel salt and Jatta gypsum in North-West Frontier Province, and Kuldana or Mami Khel red beds in North-West Frontier Province and northern Punjab (Meissner et al., 1975), is thought to have been deposited during the latest Ypresian low-sea stand of Haq et al. (1987; see Fig. 8 here).

mation with the overlying lower Miocene Chitarwata Formation (Hemphill and Kidwai, 1973; Downing et al., 1993) is a disconformity and much or all of late Eocene and Oligocene time is lost in this hiatus. Stratigraphic names used here are those of Hemphill and Kidwai (1973) and Shah (1977, 1991).

The Rakhi Nala section is well studied because of its accessibility. The early-to-middle Eocene part of this section of interest here has been studied by Eames and Nagappa (in Eames 1951, 1952a, 1952b, 1952c), who studied the mollusks; by Rieb and

Bayliss in 1956–1957, who concentrated on collecting microfossils (section itself and ostracods published by Siddiqui, 1971; planktonic foraminiferans published by Latif, 1961, and Samanta, 1972, 1973); by Rose, Hassan, and Hartenberger (in Gingerich et al., 1979) as part of a project prospecting for fossil vertebrates; and by Bhatti et al. (1988) while mapping the Choti Bala geological quadrangle. Discrepancies in published thicknesses of the formations are all small (Table 1), due to differences in beds chosen as boundaries between formations, differences in precise location where sections were measured, and differences in methods of measurement. These studies and others (Haq, 1967, 1972a, 1972b; Köthe et al., 1988) provide the basic biostratigraphic framework used to correlate the Rakhi Nala section to the geological time scale.

The lithological pattern that stands out in all descriptions of the Rakhi Nala early-to-middle Eocene section is the following: 1) Baska Formation massive fine-grained gypsum or alabaster evaporite deposits, indicating major regression (and possibly some subaerial exposure). This is overlain by 2) Habib Rahi Formation alternating platy limestones with brown and black chert interbedded with green clay shales, indicating relatively deep-water deposition with clastic input (clay) possibly controlled by Milankovich cycles of continental weathering. The spacing of Habib Rahi Formation platy limestones increases up-section and limestone thicknesses decrease up-section until the Habib Rahi Formation has graded insensibly into overlying Domanda Formation clay shales. These 3) Domanda Formation clay shales are rich in fuller's earth and predominantly green at the base of the formation and brown to reddish brown and more silty higher up, indicating a single prolonged regression from early Habib Rahi deposition through all of Domanda deposition. The lithological transition from Domanda clay shales to 4) Pir Koh deeper-water limestone deposition is sharp, indicating a rapid return to deep-water deposition. The Pir Koh Formation gives way to 5) green and then brown and reddish-brown clay shales of the Drazinda Formation, indicating a second single, prolonged regression from early Pir Koh deposition through all or most of the Drazinda Formation. There are *Discocyclina*-filled foraminiferal limestones in the middle part of the Drazinda Formation that suggest the presence of foraminiferal shoals in relatively shallow water. The upper part of the Drazinda Formation (Eames' "Tapti beds") may indicate a brief interval of de-
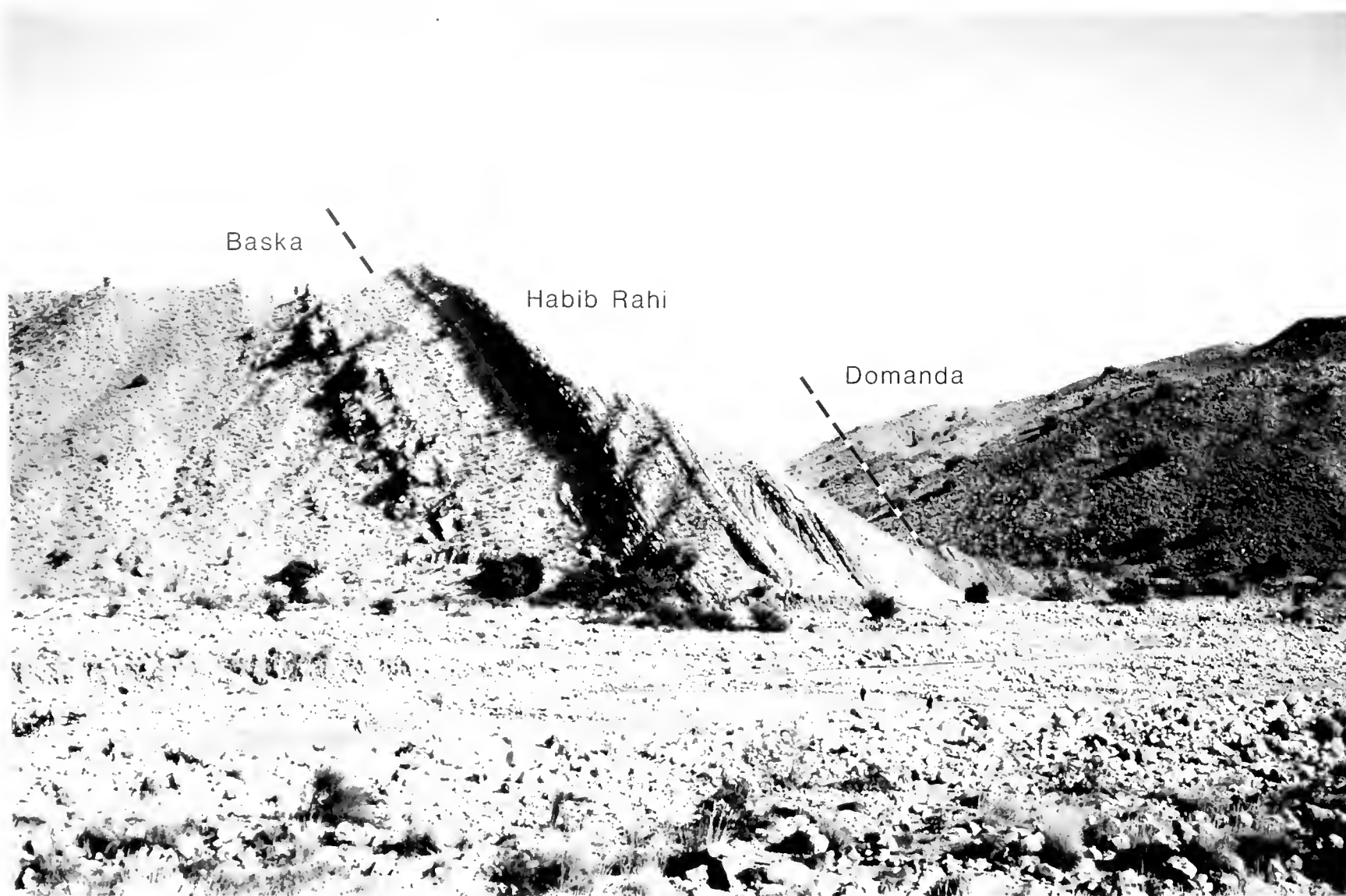
Fig. 5.—Photograph of north side of Rakhi Nala showing North Rakhi Nala section #1 of Figure 3. View is to the north. Section shows ridge-forming gypsum and softer overlying passage beds at the top of the Baska Formation, Habib Rahi Formation platy limestones, and interbedded green shales at the base of the Domanda Formation (right middle of photograph, near stream bed). The British Museum specimen of *Dalanistes ahmedi* (NHML M50719) collected by Pinfold evidently came from the low spit of green shales at the edge of Rakhi Nala (29°57'3"N latitude, 70°7'3"E longitude; Pinfold's coordinates given in his letter reprinted as Figure 2 must be erroneous because they would place the locality in Miocene Vihowa Formation much farther to the east). Search for additional parts of the specimen was unsuccessful, possibly because the original site has been eroded by flood waters. Beds here strike N20°E and dip 70°SE.

position in deeper water at the very top of the formation.

The importance of this very clear pattern of relative sea-level change is twofold: 1) it shows that a range of depositional environments are represented, suggesting changes in living environments being sampled through time (we return to this below); and 2) it invites interpretation in the context of global sea-level sequence stratigraphy (Haq et al., 1987). This in turn offers much greater chronological precision than might otherwise be possible using biostratigraphy alone. Use of the sequence-stratigraphic record within the biostratigraphic framework from Rakhi Nala allows precise correlations of the Eocene deposits in the Sulaiman Range (and their associated archaeocete faunas) to the geological time scale (Gingerich et al., 1995a, 1995b).

Baska Formation

The Baska Shale has long been considered to be the uppermost member of the Ghazij Formation, but

Shah (1991) recently raised this to formational status. Haq (1967) gave a preliminary report of limited usefulness on calcareous nannoplankton from the Ghazij shales of Zinda Pir, based on a sample collected by Y. Nagappa. Haq's more important work is that of 1972, again on calcareous nannoplankton (Haq, 1972a:7–9; 1972b:139), in which he specified that the Ghazij shale sample came from the *Marthasterites tribrachiatus* zone, nannoplankton zone NP12, of middle Ypresian age. Samanta (1972, 1973) studied planktonic foraminifera from the Rakhi Nala section and concluded that the lower and middle Ghazij Formation belong to Paleogene planktonic foraminiferal zone P8, but samples from the upper Ghazij Formation (now equivalent to the Baska Formation) were characterized by very poor preservation. Haq (1972a, 1972b) and Samanta (1972) agree in placing the lower and middle Ghazij shale in P8 and NP12, which overlap in time and include a sequence of sea-level fluctuations in the

Fig. 6.—Photograph of area north of Rakhi Nala showing general location where Barghen Nala section of Figure 3 was measured. View is to the north, with Sulaiman Range in distance at left. Highest white flatirons at left are ridge-forming Baska gypsum. These are overlain by Habib Rahi platy limestone, which also forms flatiron ridges. Ridge running through center of photograph is Pir Koh limestone. Domanda shales form the valley between Habib Rahi and Pir Koh; these can be see in cross section in small, sharply eroding nalas (dry stream beds). Shales of lower Drazinda Formation form the valley in the right center of the photograph. Ridges at right margin of photograph are *Discocyclina* limestones. An attempt was made to mine a thin bed of upper Domanda lignite located at 29°57′40″N latitude, 70°7′28″E longitude, which is just to the right of center in this photograph, behind (and stratigraphically below) the ridge of Pir Koh limestone.

middle and late Ypresian (Haq et al., 1987). Köthe et al. (1988) placed the overlying Habib Rahi limestones in late NP14 and early NP15 (see below), which is correlative with the high-sea stand in sealevel cycle TA3.2 in the early Lutetian (Haq et al., 1987). These two ages bracket the massively bedded gypsum in the Baska formation (Fig. 4), which is interpreted to represent the major sea-level fall at the end of the Ypresian. This means that the Baska Formation was deposited during latest Ypresian time.

Habib Rahi and Domanda Formations

The rhythmically-bedded Habib Rahi Formation overlies the Baska Formation in Rakhi Nala and contains closely-spaced platy limestones with brown and black cherts, alternating with green shales that thicken upward, making a smooth transition to Domanda shales as the platy limestones

become thinner and finally disappear (Fig. 5). The Domanda Formation, the formation yielding the most archaeocetes to date, was deposited on a passive continental margin on the northwestern flank of the Indo–Pakistan subcontinent before final closure of Tethys and uplift of the Himalayas. Within the Domanda Formation there is a clear transition from green shales to green and brown shales to redbrown shales. Taken together, these lithological changes indicate a shallowing-upward cycle of marine regression from the Habib Rahi Formation through the Domanda Formation.

Köthe et al. (1988) studied calcareous nannoplankton and dinoflagellates from the Rakhi Nala section and analyzed three samples from the Habib Rahi Formation. Their analysis concluded that the Habib Rahi Formation is late nannoplankton zone NP14 to early NP15 (Köthe et al. 1988:25, fig. 17). Haq (1972a, 1972b) studied the nannoplankton

Fig. 7.—Photograph of Pir Koh "white marl" or limestone where this intersects Rakhi Nala at the base of north Rakhi Nala section #2 (29°56′58″N latitude, 70°7′11″E longitude). View is to the north. Beds here strike N17°E and dip 65°SE. Upper right part of photograph is lower and middle Drazinda Formation with ridges of *Discocyclina* limestone.

from two sites in the Domanda Formation and concluded that it was probably from the *Chiphragmalithus quadratus* zone, NP15. Combining the sequence stratigraphic and biostratigraphic informa-

tion suggests that the Habib Rahi Formation is correlative with the high-sea stand in sea-level cycle TA3.2 in the early Lutetian, and the Domanda Formation is consistent with deposition during the middle Lutetian as a shelf-margin wedge during regression following the Habib Rahi high stand.

Pir Koh and Drazinda Formations

The top of the Domanda Formation is marked by a sharp lithological change, and is overlain by a second regressive cycle of deeper-water Pir Koh limestone shailowing upward through green and red-brown Drazinda shales (Fig. 6, 7). Köthe et al. (1988:25, fig. 17) studied two samples from the Pir Koh white marl band for calcareous nannoplankton and dinoflagellates and concluded that it is in nannoplankton zone NP15. This is consistent with deposition during the high-sea stand in sea-level cycle TA3.3 of the middle Lutetian (Haq et al., 1987). Köthe et al. (1988) also analyzed seven samples from the Drazinda Formation and concluded that the "*Discocyclina* marl" overlying the Pir Koh Formation includes NP16 at the base but is mostly NP17 of Bartonian age; and the uppermost part of the Drazinda is in NP18–NP19/20 of Priabonian age. Haq analyzed an assemblage from two sites in the upper Drazinda Formation and concluded that it is probably from the *Discoaster tani nodifer* zone, NP16, of late Lutetian age. Reference to the Rieb and Bayliss section and sample numbers published by Siddiqui (1971), shows that Samanta (1972, 1973) analyzed samples for planktonic foraminifera from the lower Drazinda, "upper" Drazinda with *Discocyclina*, and "*Pellatispira*" or Tapti beds, which he interpreted as belonging to Paleogene zones P12–13, P14, and P15–17, respectively. Studies in India are also relevant for dating the *Discocyclina* interval of the lower and middle Drazinda

Table 1.—*Thicknesses of middle Eocene formations in Rakhi Nala as measured by five independent field parties (Eames, 1952a:163; Rieb and Bayliss in Siddiqui, 1971; Rose, Hassan, and Hartenberger in Gingerich et al., 1979:108; and Bhatti et al., 1988:15–18). Note general similarity of formational thicknesses in all studies: discrepancies can be attributed to slight differences in beds chosen as boundaries between formations, differences in precise location where sections were measured, and differences in methods of measurement.*

	Thickness (m)				
	Eames and Nagappa 1943	Rieb and Bayliss 1956–1957	Rose et al. 1977	Bhatti et al. 1985–1986	This study 1994
Drazinda (upper chocolate clays)	297	291	—	225	331
Pir Koh (white marl band)	12	9	—	8	12
Domanda (lower chocolate clays)	283	200	297	208	303
Habib Rahi (platy limestones)	21	27	—	21	43
Baska (shales with alabaster)	229	141	—	55	122
Total	842	668	—	517	811

Formation, which was first found in Kutch (Nuttall, 1926a, 1926b).

Discocyclina is found in the Babia Stage of Biswas (1965, 1992), which includes the interval yielding archaeocetes described by Sahni and Mishra (1972, 1975) and Kumar and Sahni (1986). In the principal reference section in the Berwali stream section at Harudi, where the Harudi and Fulra formations of the Babia Stage are reported as being 40 m thick, archaeocetes come from the interval between about 7.5 and 12.5 m within this (Sahni and Mishra, 1975:5). The same section is published at almost the same scale by Mohan and Soodan (1970: 39). Comparison of these two sections shows the relevant archaeocete-bearing interval to be at or near the base of the *Globigerinoides kugleri–Globigerina frontosa* or *Globorotalia lehrneri* Paleogene planktonic foraminiferal zone (P12). Singh and Singh (1991) studied calcareous nannoplankton in the Rato Nadi stream section at Harudi, where the Harudi and Fulra formations are reported as being about 20 m thick. The lower part of the Harudi Formation did not yield calcareous nannoplankton, but the upper part of the Harudi section, and by inference the entire whale-bearing Harudi–Fulra transgressive phase, is attributed to Paleogene nannofossil zones NP16 and CP14a (Singh and Singh, 1991:30). Haq (1972a, 1972b) placed upper Drazinda shales in NP16, while Köthe et al. (1988) concluded some of the *Discocyclina* limestones at the base of the Drazinda were NP16 but most of the Drazinda was NP17 or even NP18 and NP19/20 (which is also consistent with Samanta's study of the planktonic foraminifera). Köthe et al.'s and Samanta's interpretation would span such major changes in sea level (Haq et al., 1987) that it is difficult to see how these would not be reflected in more obvious ways in the sedimentary record, and study of *Discocyclina*-bearing strata in Kutch indicating that these belong in NP16 (Singh and Singh, 1991) casts further doubt on the records of NP18 and NP19/20 from the Drazinda Formation. Thus, on the basis of both planktonic foraminifera and nannoplankton from correlative strata in Kutch, the age of *Discocyclina*-rich limestones in the Sulaiman Range would appear to be middle to late Lutetian (P11–P12 and NP15–NP16).

Although the age of the upper Drazinda Formation is uncertain due to the late Eocene and Oligocene depositional and/or erosional hiatus, the green shales with marls and limestones at the very top of the Drazinda Formation suggest deeper-water deposition and it is conceivable that this deepening is

the high-sea stand in sea-level cycle TA3.5, which is correlated with NP17 (Haq et al., 1987).

Magnetostratigraphy

We attempted to test biostratigraphic and sequence stratigraphic correlation of Sulaiman Range formations to the time scale of Haq et al. (1987) by documenting the paleomagnetic reversal stratigraphy of the Rakhi Nala stratigraphic section in Figure 3. This appeared to be a promising test because late Ypresian and Lutetian polarity reversals are few in number and widely spaced in time (Fig. 8).

A total of 389 oriented paleomagnetic samples from 103 sites were collected to document the paleomagnetic reversal stratigraphy of the Baska, Habib Rahi, Domanda, Pir Koh, and Drazinda formations (347 samples came from 93 sites in Rakhi Nala, and 42 samples came from ten sites in Takra Daab). Sixty-four limestone samples were analyzed using thermal demagnetization in a pilot investigation. Natural remanent magnetization was very weak (mean J_0 = 0.33 Ma/m), and characterized by nonbedding-corrected coordinates consistent with the present-day pole (Fig. 9A). Most samples were too weak to provide any stable demagnetization. Samples that did show stable behavior during demagnetization were generally characterized by low unblocking temperatures (below 400° C), and these produced nonbedding-corrected directions consistent with the present-day pole (Fig. 9B, C).

These results suggest that Eocene limestones in the Sulaiman Range carry weak present-day magnetization and little if any primary (Eocene) magnetization. Limestones represent only a small fraction of the total thickness of the Eocene section in this area, but they represent a large fraction of the total interval of time. Consequently, any magnetic polarity record that excluded limestones would be very incomplete and difficult to interpret.

Summary

Taking all of the lithological and microfossil evidence together provides a coherent interpretation in terms of sea-level sequence stratigraphy. Baska gypsum is most plausibly interpreted as having been deposited during the low-sea stand at the end of the Ypresian, correlative with deposition of Bahadur Khel salt and Jatta gypsum in North-West Frontier Province, and Kuldana or Mami Khel red beds in North-West Frontier Province and northern Punjab (Meissner et al., 1975). Passage beds record some sea-level fluctuation in the transition to deeper water

of the Habib Rahi high-sea stand. The Domanda Formation represents deposition with increasing continental clastic influence in a shallowing sea completing a cycle of transgression followed by regression. The Pir Koh limestones represent a second high-sea stand. This was followed in turn by the Drazinda Formation representing deposition with increasing continental clastic influence in a shallow-ing sea, completing a second cycle of transgression followed by regression. Harudi Formation fossils from Kutch correlate with this second cycle of transgression followed by regression. It is possible that the "Tapti" green shales and marls at the top of the Drazinda Formation reflect a third high-sea stand, with the record of everything that followed being erased by erosion.

MARINE MAMMAL FAUNAS

A total of six archaeocete faunas are recognized in Pakistan and these can be put into a temporal framework using the stratigraphic framework outlined above. The two oldest archaeocete faunas of Pakistan come from Kohat and northern Punjab: 1) the *Pakicetus* fluvial fauna comes from the lower Kuldana Formation, which we have correlated to the low-sea stand during the latest Ypresian (about 49.0 to 49.5 million years before present on the Haq et al. time scale); and 2) the *Ambulocetus* transitional-marine fauna comes from the upper Kuldana Formation and overlying Kohat Formation, which we have correlated to the earliest Lutetian (about 49.0 to 48.0 Ma). The former fauna is found in Kohat District of the North-West Frontier Province and in the Kala Chitta Range of northern Punjab (Gingerich et al., 1983), and the two faunas are found in superposition in the Kala Chitta Range of northern Punjab (Thewissen et al., 1994). The *Pakicetus* fauna includes *Ichthyolestes*, named by Dehm and Oettingen-Spielberg (1958), and *Pakicetus*, named by Gingerich and Russell (1981). *Ichthyolestes* has also been reported from Indian Kashmir (Kumar and Sahni, 1985). The *Ambulocetus* fauna includes *Ambulocetus*, named by Thewissen et al. (1994), and several additional taxa that are as yet poorly known. The *Pakicetus* fauna, as now known, is reviewed by Thewissen and Hussain (1998).

Four succeeding faunas come from the Sulaiman Range in southwestern Punjab: 3) the Habib Rahi Formation deep-shelf marine fauna comes from platy limestones which we have correlated to the early Lutetian (about 48.0 to 46.5 Ma), 4) the lower Domanda Formation *Rodhocetus–Takracetus* middle-shelf marine fauna comes from green clays and limestones which we have correlated to the early middle Lutetian (about 46.5 to 46.0 Ma), 5) the middle Domanda Formation *Gaviacetus–Remingtonocetus–Dalanistes* shallow shelf marine fauna comes from brown clays which we have correlated to the middle Lutetian (about 46.0 to 45.5 Ma), and 6) the middle Drazinda Formation *Babiacetus–Protosiren* shallow-shelf marine fauna comes from green clays which we have correlated to the late middle Lutetian (about 43.5 Ma). Use of a different time scale (e.g., Berggren et al., 1992; or Cande and Kent, 1992) might change the value of each calibration slightly but it will not change the geological age for any of the faunas nor the ca. 6 million-year duration of the composite sequence.

The first of the Sulaiman faunas, the Habib Rahi fauna, is rich in well-preserved fish fossils (Rahman and Dunkle, 1966), and has yielded a well-preserved, partially articulated skeleton of a new protocetid archaeocete (Gingerich, 1991; not yet studied in detail), that appears to be intermediate in morphology between earlier *Pakicetus* and later protocetids.

The best known Sulaiman faunas are those from the lower Domanda Fomation (*Rodhocetus–Takracetus* fauna) and the middle Domanda Formation (*Gaviacetus–Remingtonocetus–Dalanistes* fauna). Some remains have been known for more than 50 years (Pilgrim, 1940), but these are fragmentary, were published as representing land mammals, and cannot at present be related to lower or middle parts of the Domanda Formation. Finds made in 1981, interpreted in the light of discoveries in Kutch in India (Sahni and Mishra, 1972, 1975; Satsangi and Mukhopadhyay, 1975; Kumar and Sahni, 1986), showed that the Domanda Formation has the potential to yield well-preserved archaeocetes, but these were insufficient to suggest that differences exist between lower and middle Domanda faunas.

Differences between the lower and middle Domanda faunas were perceived in 1992 when the type specimen of *Rodhocetus kasrani* was found in lower Domanda green shales (Fig. 10). This type specimen is a largely articulated axial skeleton with skull and lower jaws, cervical, thoracic, lumbar, sacral, and proximal caudal vertebrae, ribs, left and right pelvic bones, and a right femur (Fig. 11). Here the
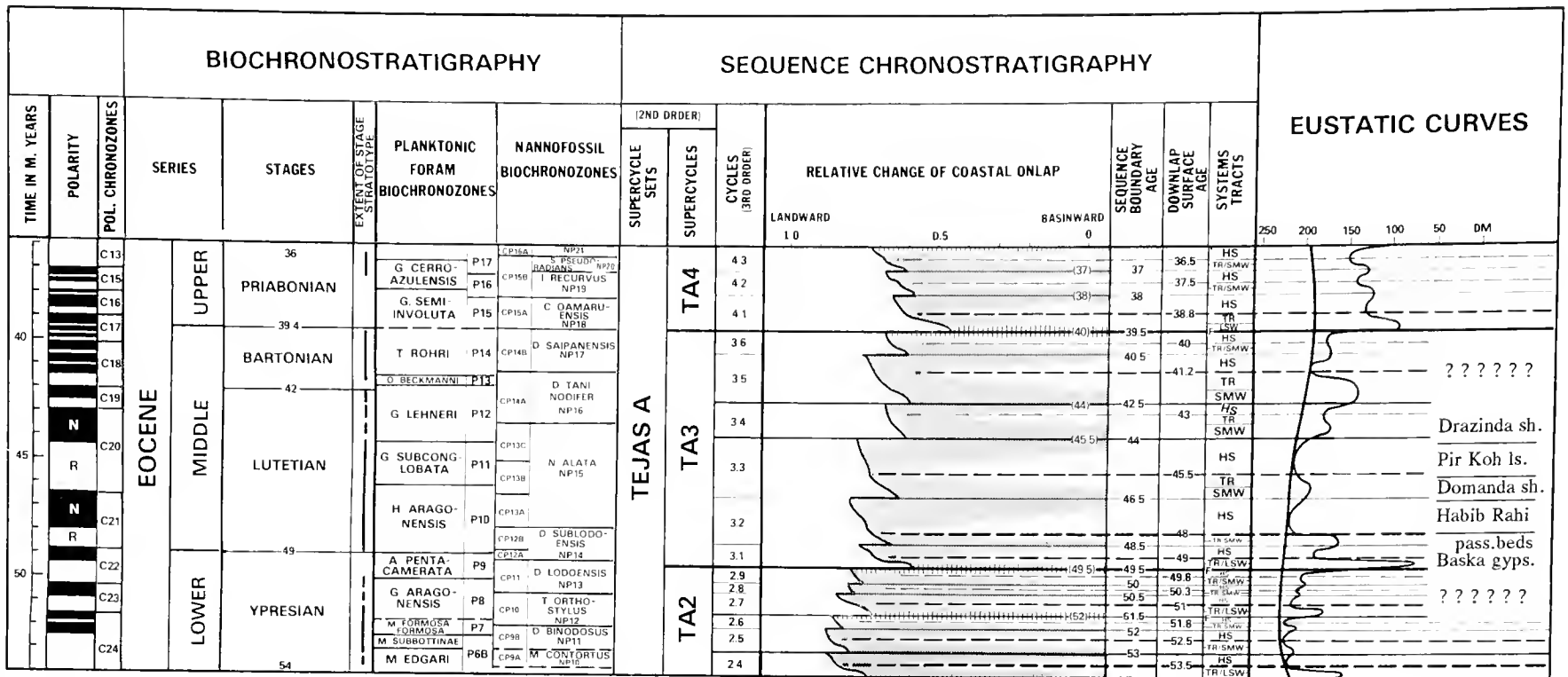
			BIOCHRONOSTRATIGRAPHY					SEQUENCE CHRONOSTRATIGRAPHY							EUSTATIC CURVES
TIME IN M. YEARS	POLARITY	POL. CHRONOZONES	SERIES	STAGES	EXTENT OF STAGE STRATOTYPE	PLANKTONIC FORAM BIOCHRONOZONES	NANNOFOSSIL BIOCHRONOZONES	SUPERCYCLE SETS	SUPERCYCLES	CYCLES (3RD ORDER)	RELATIVE CHANGE OF COASTAL ONLAP	SEQUENCE BOUNDARY AGE	DOWNLAP SURFACE AGE	SYSTEMS TRACTS	
40		C13 C15 C16 C17	EOCENE UPPER	PRIABONIAN 36 / 39.4		G CERRO-AZULENSIS P17, P16; G SEMI-INVOLUTA P15	CP16A NP21; CP15B S PSEUDO RADIANS NP20; I RECURVUS NP19; C OAMARUENSIS NP18 CP15A	TEJAS A	TA4	4.3 4.2 4.1		37 38	36.5 37.5 -38.8	HS TR/SMW HS TR/SMW HS TR LSW	??????
45	N R N R	C18 C19 C20 C21	MIDDLE	BARTONIAN 42		T ROHRI P14; O BECKMANNI P13; G LEHNERI P12	D SAIPANENSIS NP17 CP14B; D TANI NODIFER NP16 CP14A		TA3	3.6 3.5 3.4		(44) -42.5	-39.5 -40 -41.2 43	HS TR/SMW HS TR SMW HS TR SMW	Drazinda sh.
			LUTETIAN		G SUBCONGLOBATA P11; H ARAGONENSIS P10	N ALATA NP15 CP13C/CP13B/CP13A			3.3 3.2		(45.5) -44	-45.5	HS TR SMW HS	Pir Koh ls. / Domanda sh. / Habib Rahi
50		C22 C23 C24	LOWER	49 / YPRESIAN / 54		A PENTA-CAMERATA P9; G ARAGO-NENSIS P8; M FORMOSA FORMOSA P7; M SUBBOTTINAE; M EDGARI P6B	D SUBLODOENSIS NP14 CP12B; NP14 CP12A; D LODOENSIS NP13 CP11; T ORTHOSTYLUS NP12 CP10; D BINODOSUS NP11 CP9B; M CONTORTUS NP15 CP9A		TA2	3.1 2.9 2.8 2.7 2.6 2.5 2.4	(49.5) (52)	-49.5 50 50.5 51.5 52 53	-48 -49 -49.8 -50.3 -51 -51.8 -52.5 -53.5	TR/SMW HS TR/LSW HS TR/SMW TR/LSW HS TR/SMW HS TR/LSW	pass. beds Baska gyps. / ??????

Fig. 8.—Correlation chart showing inferred ages of Baska gypsum and passage beds and Habib Rahi, Domanda, Pir Koh, and Drazinda formations in relation to sea-level sequence stratigraphy of Haq et al. (1987). Thicknesses of formations composed of different lithologies are not always proportional to temporal duration of deposition. Habib Rahi and Pir Koh limestones are relatively thin in the field but represent a considerable duration of time because they are high-stand deposits that accumulated offshore and have relatively little clastic influx; while Baska, Domanda, and Drazinda shales are relatively thick in the field but represent much less time than their thicknesses would suggest because they were deposited closer to shore and are predominantly clastic in composition. Correlation of formations studied here is shown in rightmost column of chart.

cervicals are relatively short, indicating a relatively short neck by comparison with that of *Remingtonocetus*. The sacrum has four vertebral centra, distinguished in having typical sacral articulations between pleurapophyses, but these centra are not fused together like those of land mammals and contemporary remingtonocetids. Rather, the sacrals are free to move relative to each other like more-posterior caudals, indicating evolutionary "caudalization" of the sacrum and lumbus, giving them mobility like that found in later archaeocetes and required for efficient cetacean tail-powered swimming. The sacrum has auricular facets indicating direct articulation with the pelvis. The femur is short but well formed and functional, with condyles for articulation with a substantial tibia (not found). Well-developed hind limb elements suggest that *Rodhocetus* was able to support its weight and move on land, although its unfused sacrum would limit the power and range of locomotion on land. *Takracetus simus* is presently known only from a cranium with a distinctively broad palate, which was found in lower Domanda green shales. This indicates some trophic diversification of early Domanda archaeocetes but it is otherwise not very informative.

The first protocetid archaeocete found in the mid-

dle Domanda Formation was found in 1994. This form, *Gaviacetus razai*, has a distinctively narrow palate, again indicating trophic specialization. *Gaviacetus* has an associated sacral vertebra consisting of a single centrum with broad transverse processes for articulation with a pelvis (not found). The sacrum is well preserved and there is no indication of fusion to a succeeding vertebral centrum nor articulation with its pleurapophyses. Thus the sacrum included a single centrum, like that of *Protocetus*, and there was probably even more mobility in such a functionally "caudalized" vertebral column than was present in *Rodhocetus*. It seems likely that *Gaviacetus*, like *Rodhocetus* and *Protocetus*, could support its weight and move on land.

Two associations of cranial fragments and postcranial remains from the middle Domanda Formation were identified (misidentified) in 1992 as *Indocetus ramani* (Gingerich et al., 1993). These were later recognized as pertaining to *Remingtonocetus* cf. *R. harudiensis* by Gingerich et al. (1995a) when better comparative material was available. The most important elements of these finds are: 1) long cervical vertebrae, indicating that *Remingtonocetus* had a longer neck than contemporary protocetids; 2) a large land-mammal-like sacrum composed of four sacral vertebrae that are solidly fused together, in-
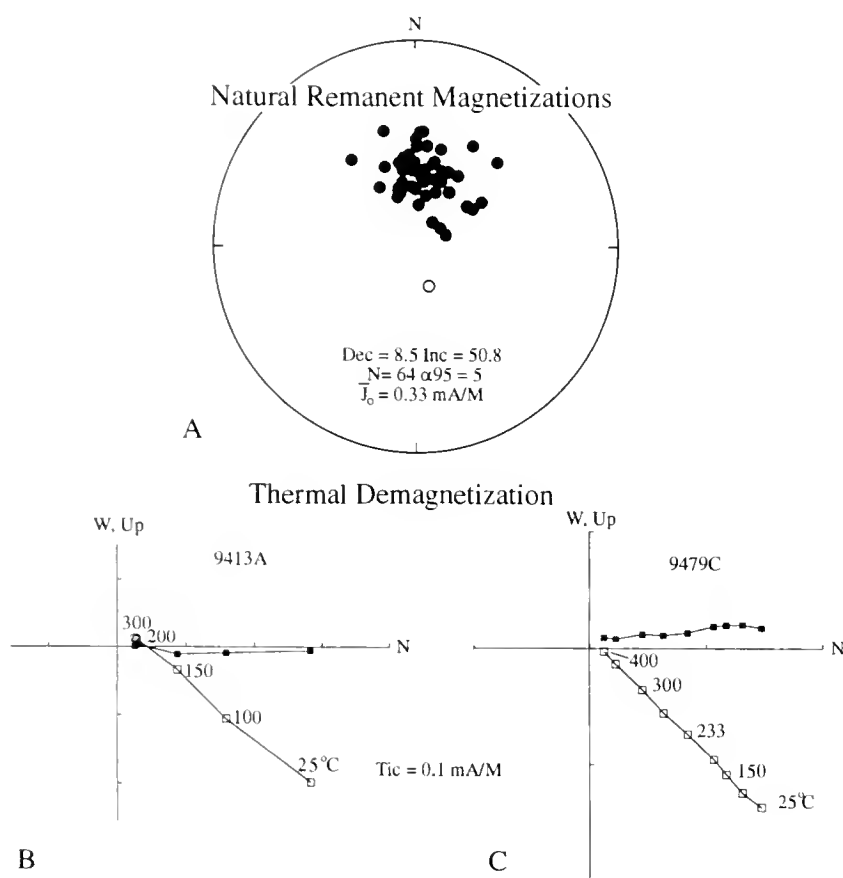
Fig. 9.—Paleomagnetic analysis of limestone samples from the Rakhi Nala section. A. Geographic coordinates (no bedding correction) of the natural remanent magnetizations (NRM) for 64 pilot samples analyzed. Samples have very low initial intensities, and directions consistent with the present-day pole. B, C. Zijderveld diagrams for two samples with stable behavior showing geographic coordinates during thermal demagnetization. Notice low unblocking temperatures, and directions consistent with the present-day pole. These results suggest the presence of a weak magnetic carrier with low unblocking temperatures bearing present-day magnetization.

dicating that *Remingtonocetus* lacked the lumbocaudal vertebral mobility of protocetids; and 3) a pelvis with auricular facets indicating direct articulation with the sacrum, and a large acetabulum, large femur, and long tibia indicating that *Remingtonocetus* retained a large hind limb capable of supporting and moving the body on land.

In 1994 a second remingtonocetid, *Dalanistes ahmedi*, was found in both lower and middle Domanda localities, but it is more common in the middle Domanda Formation. *Remingtonocetus* and *Dalanistes* have crania that are some six times longer than they are broad across the frontals, and both have preorbital rostra that are more than 60% of total skull length. Both have scapanoid or shovel-shaped frontals, relatively small orbits, ventrally convex palates, and loosely-attached exoccipitals that taper ventrally. *Dalanistes* differs from *Remingtonocetus* in being some 20% larger; having external nares open above C[1] rather than P[1]; having much higher sagittal and nuchal crests, with the rostrum distinct-

ly angled downward relative to the orientation of the braincase (clinorhynchy); retaining an open mandibular symphysis (synarthrosis) that ends at P_3 rather than P_4; and having mandibular canals in left and right dentaries separate throughout their length. Some other distinctive features of *Dalanistes*, like the deep ventral midline keel formed by left and right palatine–pterygoids and the broad tympanic–paroccipital synchondrosis, may be found in *Remingtonocetus* when better specimens are known. Postcranially, *Dalanistes* has long cervical centra that are larger but otherwise seemingly identical to those of *Remingtonocetus*. The fused sacrum, pelvis, and well-developed hind limbs of *Dalanistes* appear to have been very similar to those of *Remingtonocetus*, suggesting that it too was capable of supporting the body with the hind limbs for significant locomotion on land.

Skulls of the five archaeocetes, three protocetids and two remingtonocetids, now known from the lower and middle Domanda Formation are compared in Figure 12, which shows their differing rostral proportions and, by interpretation, trophic specializations. Among protocetids, *Takracetus* has the broadest rostrum, *Rodhocetus* has a rostrum of intermediate breadth, and *Gaviacetus* has the narrowest rostrum. The two remingtonocetids are similar in rostral proportions, but differ from all of the protocetids in being more needle-nosed. Broader-nosed archaeocetes may have fed on larger fishes, while narrower-nosed archaeocetes may have fed more selectively on smaller fishes, but details of possible specialization cannot, as yet, be suggested. When hind limb differences are considered, protocetids appear to have been more pursuit-oriented, while remingtonocetids may have been ambush-predators. There is a tendency, too, for protocetids to be found in deeper-water sediments of the lower Domanda Formation, while remingtonocetids predominate in shallower-water sediments of the middle Domanda Formation, which is consistent with the former being more efficient swimmers able to range farther offshore.

The middle Drazinda Formation *Babiacetus–Protosiren* shallow-shelf marine fauna is younger than the Domanda faunas described here, but it has not yet been sampled well enough to permit any generalization about it. The only archaeocete known to date, a protocetid skull and lower jaws described by Gingerich et al. (1995b), is evidently the same as *Babiacetus indicus*, named by Trivedy and Satsangi (1984) from Kutch in India. *Protosiren sattaensis* is found in the Drazinda Formation

Fig. 10.—Type locality of *Rodhocetus kasrani* before excavation (30°46'06"N latitude, 70°26'37"E longitude). When found, all that was showing of the type specimen (Fig. 11) was the ventral margin of a dentary (white pieces of bone to left of glue bottles in foreground). This locality is in Bozmar Nadi (Fig. 1). Lithology is green clay shale of the lower Domanda Formation, with 1–5 mm-thin layers of gypsum mobilized during folding of the Zinda Pir anticlinorium. View is to the south, and the ridge in the background is a Habib Rahi Formation dip-slope at the northern plunge of the Rodho anticline. Bottles and brush give the scale in the foreground, and the collector on the ground in the right center of the photograph gives the scale in the middle distance.

(Gingerich et al., 1995b), and it, or some closely related species, is also found in Kutch (Bajpai et al., 1989). If the vertebrate fauna of the Pir Koh and Drazinda sea-level cycle is the same as that of Kutch (Sahni and Mishra, 1972, 1975; Kumar and Sahni, 1986) then we should expect to find the protocetid *Indocetus ramani* and the remingtonocetids *Remingtonocetus harudiensis* and *Andrewsiphius*

kutchensis in the Drazinda Formation in addition to *Babiacetus*.

The Drazinda Formation fauna is evidently younger than the long-known Egyptian *Protocetus–Protosiren* fauna of Gebel Mokattam (ca. 45.0 Ma; Gingerich, 1992), and the Indian *Indocetus–Remingtonocetus* fauna from Kutch probably lies in the range spanned by these two (ca. 45.0 to 43.5 Ma). *Rod-*
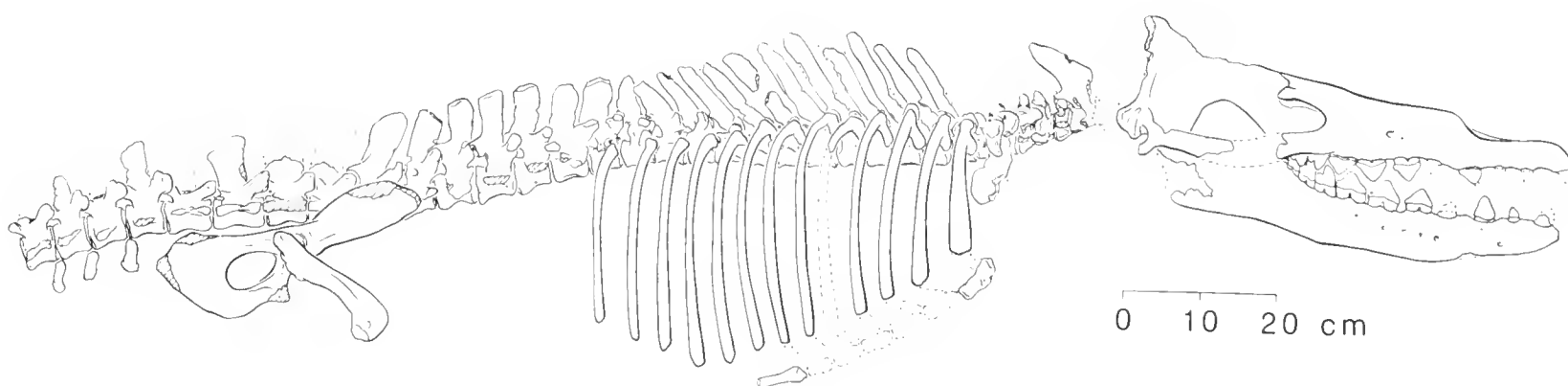
Fig. 11.—Skeleton of protocetid *Rodhocetus kasrani* (GSP-UM 3012, holotype) from the lower Domanda Formation (type locality shown in Figure 10). Note relatively short cervical vertebrae and neck, high neural spines on thoracic vertebrae, sacrum composed of four centra with pleurapophyseal articulations but no fusion, relatively large femur and pelvis articulating with sacrum, and base of heavy tail. Figure from Gingerich et al. (1994).
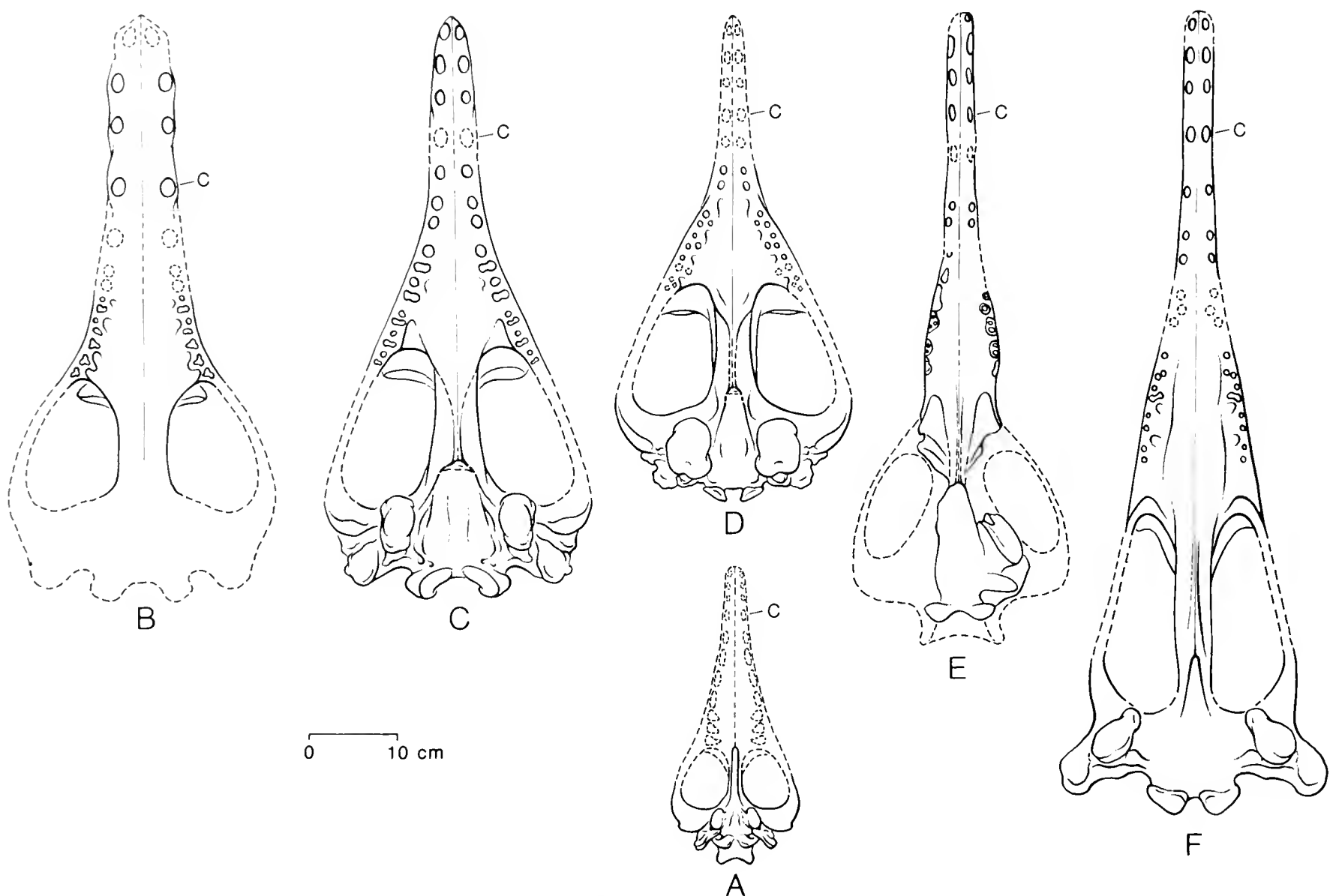
Fig. 12.—Comparison of the skull of late Ypresian *Pakicetus* (A) from the Kuldana Formation of Kohat District, North-West Frontier Province, with five skulls of later archaeocetes from the middle Lutetian Domanda Formation of the Sulaiman Range, southwestern Punjab. The five Domanda archaeocetes are the protocetids *Takracetus* (B), *Rodhocetus* (C), and *Gaviacetus* (D), and the remingtonocetids *Remingtonocetus* (E) and *Dalanistes* (F). Morphological diversity in the Sulaiman Range fauna from the Domanda Formation is greater than that known to date from any other time or place in the history of archaeocetes, but this may change as the younger Pakistan Drazinda Formation and Indian Harudi-Fulra Formation archaeocete faunas become better known. The well-known middle-to-late Eocene (latest Bartonian and Priabonian) archaoecete faunas of Egypt include a similar number of taxa, but all have very stereotyped skulls that vary little from taxon to taxon.

hocetus, *Protocetus*, and *Indocetus* are difficult to tell apart from skulls alone, but the pelves of *Rodhocetus* and *Protocetus* are very different, and it is likely that these both differ from *Indocetus* as well (although this awaits confirmation by discovery of more nearly complete postcranial remains of *Indocetus* in Kutch).

DISCUSSION

The archaeocete faunas of Pakistan show several things about the early evolution of whales that were not evident before these were discovered. First, eastern Tethys was clearly part of the center of origin and diversification of early archaeocete whales. It may not have been the only center, and any such center or centers may have covered a broad area, but eastern Tethys has yielded more stages of early whale evolution than any other geographic region and it must have been part of the range in which early whale diversification was taking place.

Second, there is a much broader range of cranial and postcranial morphological diversity represented in the known Pakistan archaeocetes than there is in archaeocetes found in younger deposits elsewhere (e.g., in Egypt or southeastern North America, where later archaeocetes are well sampled). This is illustrated for the Domanda Formation by the range

Table 2.—*Differences distinguishing skulls and postcranial skeletons of middle Eocene Protocetidae and Remingtonocetidae (from Gingerich et al., 1995a, with additions).*

Protocetidae	Remingtonocetidae
Length of cranium approximately 3× breadth across frontals	Length of cranium approximately 6× breadth across frontals
Preorbital rostrum less than 60% of total skull length	Preorbital rostrum more than 60% of total skull length
Orbits medium to large in diameter relative to rest of skull	Orbits small relative to rest of skull
Nares open above C^1, P^1, or P^2	Nares open above C^1 or P^1
Frontals sphyroid or hammer-shaped	Frontals scapanoid or shovel-shaped
Incisors and anterior premolars circular in cross section and robust	Incisors and anterior premolars narrow labiolingually
Upper molars generally small and broad, with two lateral roots and a distinct medial root	Upper molars generally larger and narrow, sometimes double-rooted and lacking distinct medial root
Palate flat or concave ventrally	Palate convex ventrally
Ventral palatine–pterygoid surface flat or shallowly ridged	Ventral palatine–pterygoid surface with deep ventral midline keel
Bulla articulation with rest of skull includes a narrow paroccipital synchondrosis	Bulla articulation with rest of skull includes a broad paroccipital synchondrosis
Exoccipitals rectangular, robustly integrated with squamosal, and solidly attached to rest of skull	Exoccipitals tapering downward, loosely attached to squamosal, and separated from basioccipital by a waisted section that often breaks
Cervical centra are shorter than they are wide or high, and shorter than anterior thoracic centra	Cervical centra are as long as they are wide or high, and as long or longer than anterior thoracic centra
Sacrum is composed of four or fewer vertebral centra, with sacral centra generally not fused to each other	Sacrum is composed of four vertebral centra, with centra of S1–S3 and generally S4 solidly fused to each other
Innominate with smooth lateral surface in front of acetabulum, with a shallow acetabular fossa and no distinct acetabular notch	Innominate with distinct depression on lateral surface in front of acetabulum, with a deep acetabular fossa and a distinct acetabular notch
Femoral head with distinct, deep fovea for round ligament	Femoral head with shallow or indistinct fovea for round ligament
Femoral shaft round; distal femur narrow relative to shaft diameter, with a narrow, raised patellar groove	Femoral shaft oval in cross section, with lateral keel for muscle insertion; distal femur broad relative to shaft diameter, with a broad, shallow patellar groove

of cranial shapes illustrated in Figure 12, but the later "Drazinda" fauna known from Kutch may include a still greater range of forms. *Babiacetus*, for example, is larger than any protocetid known from the Domanda Formation, and *Andrewsiphius*, to take another example, is a more specialized remingtonocetid than any known from the Domanda Formation.

Third, protocetids and remingtonocetids share many features characteristic of archaeocetes, but by Domanda time these two families are clearly separated in having many distinctive cranial and postcranial specializations (Table 2). Protocetids appear to have been the more active swimmers, and to have been the ancestors of basilosaurid archaeocetes and, through dorudontine basilosaurids, the ancestors of later modern cetaceans.

Fourth, the sequence of acquisition of distinctive aquatic adaptations through time indicates that the initial specialization of archaeocetes was a trophic one, with evolution of a characteristic dentition appearing first. *Pakicetus*, the oldest archaeocete known from a skull, was found in continental red

beds with an associated land-mammal fauna. It has sharply-pointed conical anterior teeth, and long, narrow posterior premolars and molars suggestive of feeding on fish (Gingerich and Russell, 1990). *Pakicetus* can have had little ability to hear directionally in water (Gingerich et al., 1983), nor even the ability to hear well in water: *Pakicetus* has a small mandibular canal, meaning that sound reached the ear drum through the external auditory meatus as in land mammals, and its incus is intermediate between land mammals and aquatic cetaceans in inflation, crural proportions, and position of the mallear joint (Thewissen and Hussain, 1998). The postcranial skeleton of *Pakicetus* is still unknown.

The second stage of specialization of early archaeocetes involved the hearing apparatus (Luo et al., 1995). The Habib Rahi archaeocete and slightly later *Rodhocetus* (Gingerich et al., 1994) have a *Pakicetus*-like dentition with pointed anterior teeth and long, narrow posterior cheek teeth but, in addition, the auditory bullae are large and dense, and there are well-developed mandibular canals not seen in *Pakicetus* that open into a large "acoustic win-

dow" on the medial side of each dentary. These are interpreted as wave guides to aid hearing in water (Norris, 1968). There are no pterygoid fossae or accessory air sinuses associated with the bullae, so directional hearing may have been limited. Hind limbs are not yet known for the Habib Rahi archaeocete but, as stated above, *Rodhocetus* retained a sacrum, pelves, and substantial hind limbs capable of supporting its weight on land, and the Habib Rahi archaeocete probably did also. Remingtonocetids, as far as they are known at present, appear not to have progressed beyond this second stage of aquatic specialization.

The third stage of specialization of archaeocetes involved streamlining the body by shortening the neck and reducing the hind limbs, with development of cetacean-style swimming locomotion involving "caudalization" of the lumbus and sacrum associated with dorsoventral oscillation of a heavily muscled tail. *Rodhocetus* shows clear evidence of all three: cervical vertebrae are relatively short, the femur is reduced in size, and the sacral vertebrae are no longer fused into a solid sacrum. However, none of these shortenings, reductions, and disarticulations in *Rodhocetus* is carried as far as it is in later basilosaurids (Gingerich et al., 1990).

The observation that the initial aquatic adaptation was trophic supports the idea that archaeocetes entered Tethys to feed on fish in the late early Eocene when eastern Tethys was a highly productive shallow seaway of elevated salinity (Gingerich et al., 1983). One can easily imagine the opportunism of a succession of cursorial *Sinonyx-* or *Pachyaena-* like mesonychid "strandloopers" feeding first on fish carrion washing up on the shoreline, and then learning to catch live fish trapped in lagoonal pools or slower fish in shallow open water. There are two ways to do this: one is to ambush fish as remingtonocetids may have done, and the other is to pursue them as protocetids must have done. It is, of course, simplistic to think in terms of three discrete stages of aquatic adaptation. These clearly overlapped in development, and there must be many substages still to be recognized in the evolution of archaeocete feeding, hearing, and locomotion.

ACKNOWLEDGMENTS

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Note added in proof:

Correlation chart (Fig. 8) in this paper is superseded by correlation chart in Gingerich et al., 1997:fig. 14.

GINGERICH, P. D., M. ARIF, M. A. BHATTI, M. ANWAR, AND W. J. SANDERS. 1997. *Basilosaurus drazindai* and *Basilosaurus hussaini*, new Archaeoceti (Mammalia, Cetacea) from the Middle Eocene Drazinda Formation, with a revised interpretation of ages of whale-bearing strata in the Kirthar Group of the Sulaiman Range, Punjab (Pakistan). Contributions from the Museum of Paleontology, University of Michigan, 30:55–81.

A NEW GENUS OF TARSIIDAE (MAMMALIA: PRIMATES) FROM THE MIDDLE EOCENE OF SHANXI PROVINCE, CHINA, WITH NOTES ON THE HISTORICAL BIOGEOGRAPHY OF TARSIERS

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ABSTRACT

A new genus and species of Tarsiidae is described from the late middle Eocene Heti Formation, Yuanqu Basin, southern Shanxi Province, People's Republic of China. Phylogenetic analysis of dental and gnathic characters suggests that *Xanthorhysis tabrumi*, n. gen. and sp., is the sister group of the clade including all living and fossil species of *Tarsius* (including *T. eocaenus*). Cladogenesis among the principal taxa of haplorhine primates, including Tarsiidae, Omomyidae, and Anthropoidea, must have occurred early in the Paleogene.

Based on their fossil record and the geographic distribution of outgroups, Tarsiidae probably originated on the Asian mainland. Their current geographic restriction to offshore islands in south-eastern Asia is interpreted as relictual. Access to the tropical, low-latitude refugia of the Sunda Shelf and its environs during middle Cenozoic climatic deterioration was a key factor underlying the survival of Asian tarsiids to the Recent. North American and European Eocene tarsiiforms lacked similar geographical access to low-latitude refugia, and tarsiiforms were extirpated on both of these continents during this interval. Alleged records of Afro–Arabian Paleogene tarsiiforms are inadequate for inferring that tarsiiform primates ever inhabited that landmass. The great antiquity now demonstrated for Tarsiidae raises the possibility that tarsiers achieved their current geographic range on both sides of "Wallace's Line" by means of vicariance rather than over-water dispersal across the Makassar Strait.

INTRODUCTION

"Il est pourtant presque obligatoire que, durant le Tertiaire, l'Asie ait hébergé les ancêtres de l'actuel *Tarsius* (Tarsiidae), lequel ne peut dériver directement des Tarsiiformes connus en Amérique du Nord et en Europe" (Hoffstetter, 1977:335).

Tarsiers are a highly distinctive clade of living primates endemic to islands of the Sunda Shelf (including Sumatra, Borneo, and numerous smaller islands), the southern Philippines (including Mindanao, Leyte, Bohol, and Samar) and Sulawesi (Niemitz, 1984*a*; Musser and Dagosto, 1987). Anatomical and ecological specializations are well documented in tarsiers, which are unique among living primates in that they consume only live animal prey (primarily large insects such as grasshoppers, crickets, and scarabid beetles, but also such small vertebrates as lizards, frogs, and even birds; see Niemitz, 1984*b*). Tarsiers are also notable for their nocturnal activity pattern and associated adaptations of the visual apparatus (Cartmill, 1980; Castenholz, 1984; Stephan, 1984). Finally, tarsiers are quintessential vertical clingers and leapers (Niemitz, 1984*d*; Crompton and Andau, 1986), and show numerous postcranial specializations that allow for this ricochetal mode of locomotion (Jouffroy et al., 1984; Dagosto, 1985; Gebo, 1987).

The many exceptional attributes of tarsiers are often interpreted as evidence of their long phylogenetic isolation from other major groups of living primates. As such, tarsiers have played a key (yet persistently controversial) role in attempts to reconstruct higher-level primate phylogeny. To a large extent, this pivotal position of tarsiers in primate phylogeny stems from the long-standing view that tarsiers are the extant sister group of anthropoids. One widely supported systematic arrangement that reflects this notion is the suborder Haplorhini of Pocock (1918), which includes living and fossil tarsiers, anthropoids, and (variably) the extinct Omomyidae, while excluding living and extinct strepsirhine primates (lemurs, lorises, and their kin). Notwithstanding the reservations of a few subsequent workers (e.g., Gingerich, 1976; Gingerich and Schoeninger, 1977; Krishtalka and Schwartz, 1978; Schwartz and Tattersall, 1987; Shoshani et al., 1996), it is now widely accepted that tarsiers are the nearest living relatives of anthropoids (e.g., Luckett, 1975; Szalay, 1976; Cartmill, 1980; Rosenberger and Szalay, 1980; Koop et al., 1989*a*, 1989*b*; Martin, 1990; Beard and MacPhee, 1994; Goodman et al., 1994; Ross, 1994).

Despite this broad agreement on the monophyly of Haplorhini among living primates, a variety of

opinions remain on whether or not certain fossil taxa, particularly omomyids such as *Shoshonius*, belong within the clade encompassing tarsiers and anthropoids (e.g., Szalay, 1976; Hoffstetter, 1977; Cartmill, 1980; Rosenberger and Szalay, 1980; MacPhee and Cartmill, 1986; Beard and MacPhee, 1994; Fleagle and Kay, 1994; Kay and Williams, 1994; Ross, 1994). These competing phylogenies can imply highly divergent reconstructions of character evolution over the evolutionary history of tarsiers and anthropoids. For example, proponents of a strict *Tarsius* + Anthropoidea clade (excluding omomyids) argue that either 1) tarsiers have undergone numerous evolutionary reversals from a common ancestor with anthropoids that would have looked essentially like a small monkey (Cartmill, 1980), or 2) anthropoids have undergone numerous evolutionary reversals from a common ancestor with tarsiers that would have looked much more like a tarsier (Ross, 1994). A more prevalent phylogenetic hypothesis depicts *Tarsius* as the only surviving genus of a broad and diverse radiation of Eocene tarsiiforms (Szalay, 1976; Hoffstetter, 1977; Gingerich, 1981; Rosenberger, 1985; Beard et al., 1991; Beard and MacPhee, 1994). Under this latter scheme, tarsier progenitors are unlikely to have been more anthropoid-like than modern *Tarsius*, because the evolutionary transformations that led to *Tarsius* would simply entail the addition of several highly diagnostic autapomorphies onto a basic bauplan that is little changed since the early Cenozoic (Beard et al., 1991; Beard and MacPhee, 1994). Similarly, the earliest anthropoids need not have closely resembled living *Tarsius*, because many anthropoid peculiarities must have evolved in mosaic fashion along their stem lineage, after the anthropoid–tarsiiform dichotomy (cf. MacPhee et al., 1995).

One potential pitfall common to all previous studies of the evolutionary history of tarsiers is that the fossil record for Tarsiidae has been nonexistent until quite recently, and it remains meager by any standard. The first fossil tarsier, *Tarsius thailandicus*, was described in 1987 on the basis of a single lower molar from the middle Miocene of northwestern Thailand (Ginsburg and Mein, 1987; note that the original authors referred to this species as *Tarsius thailandica*, but the trivial name must be changed in accordance with the International Code of Zoological Nomenclature; see Ducrocq et al., 1994). Subsequently, much older fossil tarsiers were described as *Tarsius eocaenus* from the middle Eocene Shanghuang fissure fillings of southern Jiangsu

Province, China (Beard et al., 1994). Whereas these fossils documented what many workers had long suspected—that tarsiers are an ancient clade of primates with a long history of endemism in Asia—they also left much to be desired because all that was known of either species were isolated cheek teeth.

The purpose of this paper is to place on record a new fossil tarsiid from the middle Eocene Heti Formation, southern Shanxi Province, China, which was collected during the course of collaborative field work by the Institute of Vertebrate Paleontology and Paleoanthropology and the Carnegie Museum of Natural History. The holotype and only known specimen of this new form is the most nearly complete fossil tarsiid yet discovered. Following the description of this new taxon, I will offer a hypothesis regarding its phylogenetic position and some remarks on the historical biogeography of tarsiers.

Institutional acronyms are as follows: DPC, Duke University Primate Center, Durham, North Carolina; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, People's Republic of China.

Order Primates Linnaeus, 1758
Suborder Haplorhini Pocock, 1918
Infraorder Tarsiiformes Gregory, 1915
Family Tarsiidae Gray, 1825
Xanthorhysis, **new genus**

Type Species.—Xanthorhysis tabrumi, n. sp.; only known species.

Diagnosis.—Differs from omomyids in having relatively larger alveolus for C_1 (resulting in noticeable labial swelling of the dentary), and in having stronger, more trenchant crests running mesially and distolingually from the protoconids of P_{3-4}. Differs from *Afrotarsius* in having stronger, more cuspidate lower molar paraconids and M_3 unreduced in length. Differs from living species of *Tarsius* in having P_{3-4} relatively longer, with roots widely splayed rather than mesiodistally compressed. P_4 metaconid stronger and situated lower on the crown than in living species of *Tarsius*. Differs from living and fossil species of *Tarsius* in having lower molars relatively longer, narrower, and lower-crowned, with entoconids more distal in position. Lower molars smaller than those of *T. bancanus* and *T. syrichta*, larger than those of *T. eocaenus*.

Etymology.—Greek *xanthos* (yellow) and Greek *rhysis* (river), in keeping with the common practice of naming fossil tarsiiform genera for the major drainages in which they were first discovered.
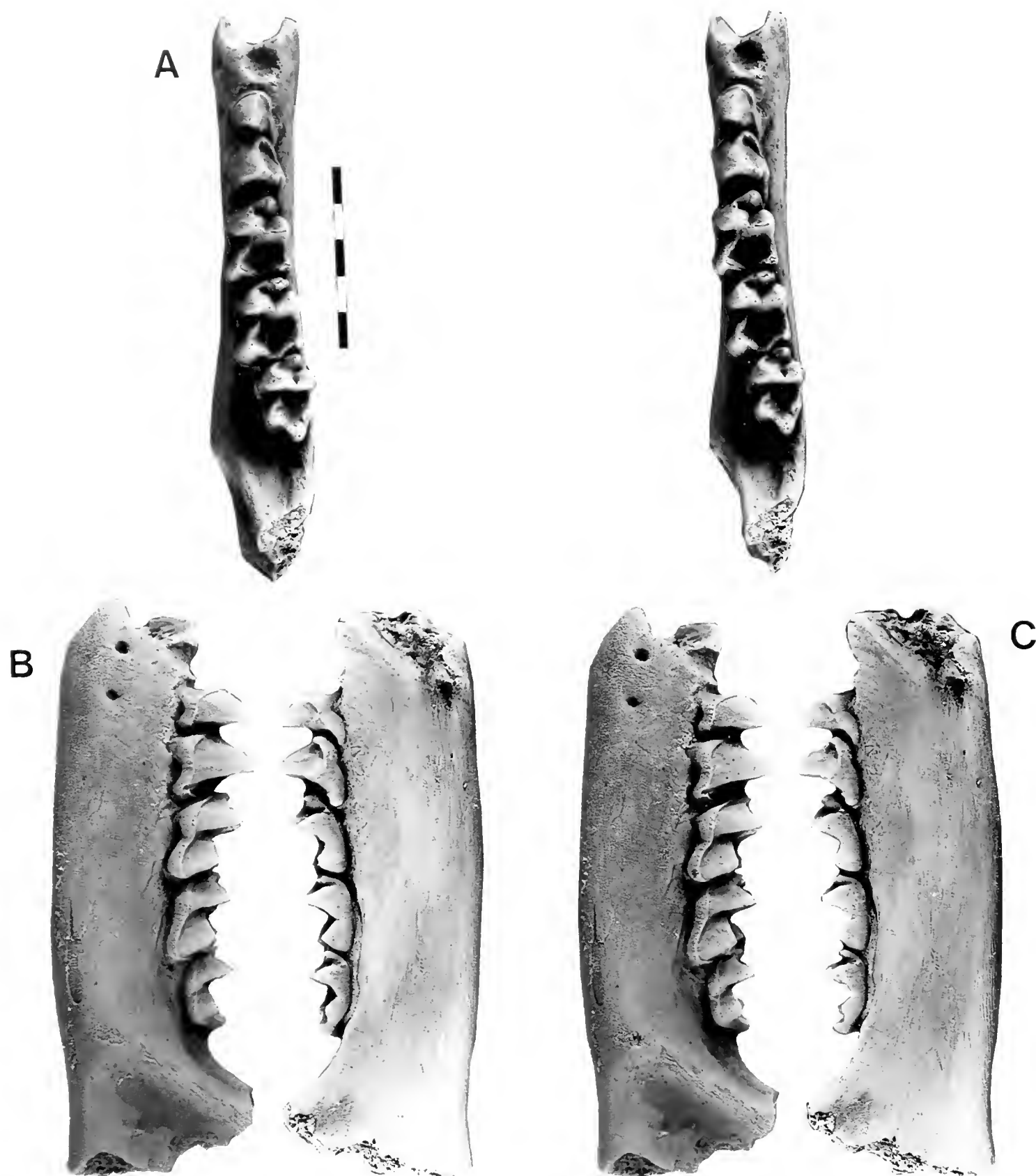
Fig. 1.—*Xanthorhysis tabrumi*, n. gen. and sp., holotype, IVPP V12063. Left dentary preserving P$_3$–M$_3$ and alveoli for C$_1$–P$_2$ in occlusal (A), buccal (B), and lingual (C) views. All views are stereopairs. Scale = 5 mm.

Xanthorhysis tabrumi, **new species**
(Fig. 1)

Holotype.—IVPP V12063 (Fig. 1), left dentary preserving P$_3$–M$_3$ and alveoli for C$_1$ and P$_2$.

Type Locality.—Drainage south of Liugou village, Yuanqu County, southern Shanxi Province, People's Republic of China: 35°7.76′N, 111°51.25′E. The ephemeral drainage in which the type locality occurs comprises an eastern tributary to the larger Baishui drainage in this area (Fig. 2).

Known Distribution.—Late middle Eocene (prob-ably Sharamurunian Land Mammal Age), Heti Formation, Yuanqu Basin, Shanxi Province, People's Republic of China.

Diagnosis.—As for the genus (currently mono-typic).

Etymology.—For Alan R. Tabrum, collector, preparator, and student of fossil mammals at the Carnegie Museum of Natural History, who discovered the only known specimen of this species on May 22, 1994.

Description.—IVPP V12063 is a left dentary fragment bearing the well-preserved crowns of P$_3$–M$_3$. Anteriorly, two alveoli are

preserved mesial to the crown of P_3. In position and relative proportions, these alveoli match those for C_1 and P_2 in living species of *Tarsius*. As in modern *Tarsius*, the alveolus for C_1 is greatly enlarged (width, 1.60 mm) and nearly vertical in orientation. The single alveolus for P_2 is much smaller (width, 0.95 mm) than that for C_1.

P_3 (length, 1.55 mm; width, 1.20 mm) is double rooted and bears a relatively simple crown. As in *Tarsius*, the apex of the protoconid is curved slightly linguad. The protoconid is adorned mesially and distolingually by well-developed crests; a much weaker crest occurs on the distolabial border of this cusp. The mesial protoconid crest is continuous from the apex of the protoconid to the lingual cingulid. The distolingual protoconid crest is equally extensive, but near the base of the crown this structure continues distally onto the weak talonid heel of P_3 rather than merging with the lingual cingulid. Cingulids, which are weak labially but stronger lingually, completely encircle the base of the crown of P_3. A prominently bevelled surface, probably corresponding to a wear facet, occurs on the mesiolabial surface of the base of the crown, inferior to the labial cingulid. The morphology of the weak talonid heel is obscured by the mesial end of P_4, which overlaps it. Overall, the crown of P_3 is strongly convex labially but virtually flat lingually. As it is now preserved, the crown appears to be tilted slightly distally, but whether this represents the true orientation of the tooth in life rather than slight postmortem deformation cannot be determined.

P_4 (length, 2.10 mm; width, 1.55 mm) is double rooted and possesses a slightly more complicated crown than does P_3. The trigonid bears cusps in both the metaconid and protoconid positions; the former cusp is situated relatively low on the crown and juts strongly lingually. The protoconid of P_4 is strongly convex labially, but slightly concave lingually. As on P_3, the apex of the protoconid of P_4 is curved linguad. A similar condition characterizes modern tarsiers. Pronounced crests run mesially, distolingually, and distolabially from the tip of the protoconid. The distolingual protoconid crest unites this cusp with the metaconid. Two weak crests run vertically up the postvallid on either side of the metaconid, defining an indistinct talonid basin. There is a complete, but poorly defined, labial cingulid. A slit-like wear facet traverses the labial cingulid immediately distal to the point of union between the distolabial protoconid crest and the labial cingulid. Lingually, a stronger cingulid runs from the metaconid to the mesiolingual end of the tooth, where a weak swelling of enamel may represent an incipient paraconid.

M_1 (length, 2.25 mm; width, 1.85 mm) possesses all three trigonid cusps, as do most living and fossil tarsiiforms. The trigonid cusps are more prominent and more strongly differentiated from one another basally than is the case in *Tarsius*, but their relative positions are similar. The talonid is wider than the trigonid and bears hypoconid and entoconid cusps of roughly equivalent size, in contrast to the condition in *Tarsius* in which the entoconid is typically reduced in comparison with the hypoconid. A small, centrally placed hypoconulid occurs on the distal margin of the talonid, but this area is slightly damaged. A cingulid completely lines the buccal margin of the crown. In occlusal outline, the buccal border of the tooth displays a weak invagination near the ectoflexid. This border is more uniformly straight in *Tarsius*. All lower molars are lower crowned in *Xanthorhysis* than is the case in extant *Tarsius*.

M_2 (length, 2.20 mm; width, 1.80 mm) differs from M_1 only in minor details of trigonid morphology. The protoconid and metaconid are more widely separated on M_2 than on M_1, and the paraconid is slightly more distal in position on M_2. The bases of the paraconid and metaconid are more broadly separated than is the case in *Tarsius*, as is also true (but to a lesser extent) for M_1. The entoconid is situated farther distally than is the case in *Tarsius*. As on M_1, a cingulid completely surrounds the buccal half of the crown.

M_3 (length, 2.35 mm; width, 1.60 mm) is unusual in having a trigonid that is noticeably wider than the talonid. As is the case for M_{1-2}, the paraconid and metaconid are broadly separated basally, in contrast to the condition in *Tarsius* and many omomyids. The paraconid is more mesial than lingual in position, also in contrast to the situation in *Tarsius*. The entoconid is situated distally, farther from the postvallid than is the case in *Tarsius*, but this cusp still lies mesial of the level of the hypoconid. The hypoconulid is simple, unicuspid, and projects distally beyond the remainder of the talonid. A weak valley separates the hypoconulid and entoconid cusps. A cingulid is virtually complete buccally, although this structure is extremely weak between the hypoconid and hypoconulid cusps and is interrupted by a conspicuous wear facet buccal to the ectoflexid.

The dentary exhibits a relatively uniform depth (3.75 mm beneath the talonid of M_1) throughout its preserved length. Two mental foramina occur on the labial aspect of the dentary, beneath the mesial part of the alveolus for P_2 and the mesial root of P_3, respectively. Only the posterior part of the symphyseal region, which is unfused, remains. The preserved part of the symphyseal region shows no evidence of bony buttressing ventrally, as is common if not ubiquitous in living *Tarsius*. Near the posteroventral end of the symphyseal region is a prominent circular depression marking the area for insertion of genioglossus. The preserved part of the masseteric fossa appears to be more deeply excavated than is the case in *Tarsius*. Living tarsiers exhibit highly characteristic specializations of the coronoid process, condyle, and angle (Musser and Dagosoto, 1987). Unfortunately, the posterior part of the dentary in IVPP V12063 is broken away, precluding determination of whether or not these distinctive features also occurred in *Xanthorhysis tabrumi*.

PHYLOGENETIC POSITION OF *XANTHORHYSIS*

Although it is known from only a single incomplete lower dentition, *Xanthorhysis* possesses several traits that distinguish it from all primates other than *Tarsius*. More distant similarities to various omomyids and the basal anthropoid *Eosimias* are also manifest, as might be expected given the close phylogenetic relationships among tarsiids, omomyids, and anthropoids advocated by many workers. Here, characters that are believed to be useful in demonstrating the tarsiid, rather than omomyid or eosimiid, affinities of *Xanthorhysis* are emphasized.

The anteriormost part of the dentary remains unknown in *Xanthorhysis tabrumi*, precluding determination of the number of lower incisors, their relative size(s), and mode of implantation. Hence, it is
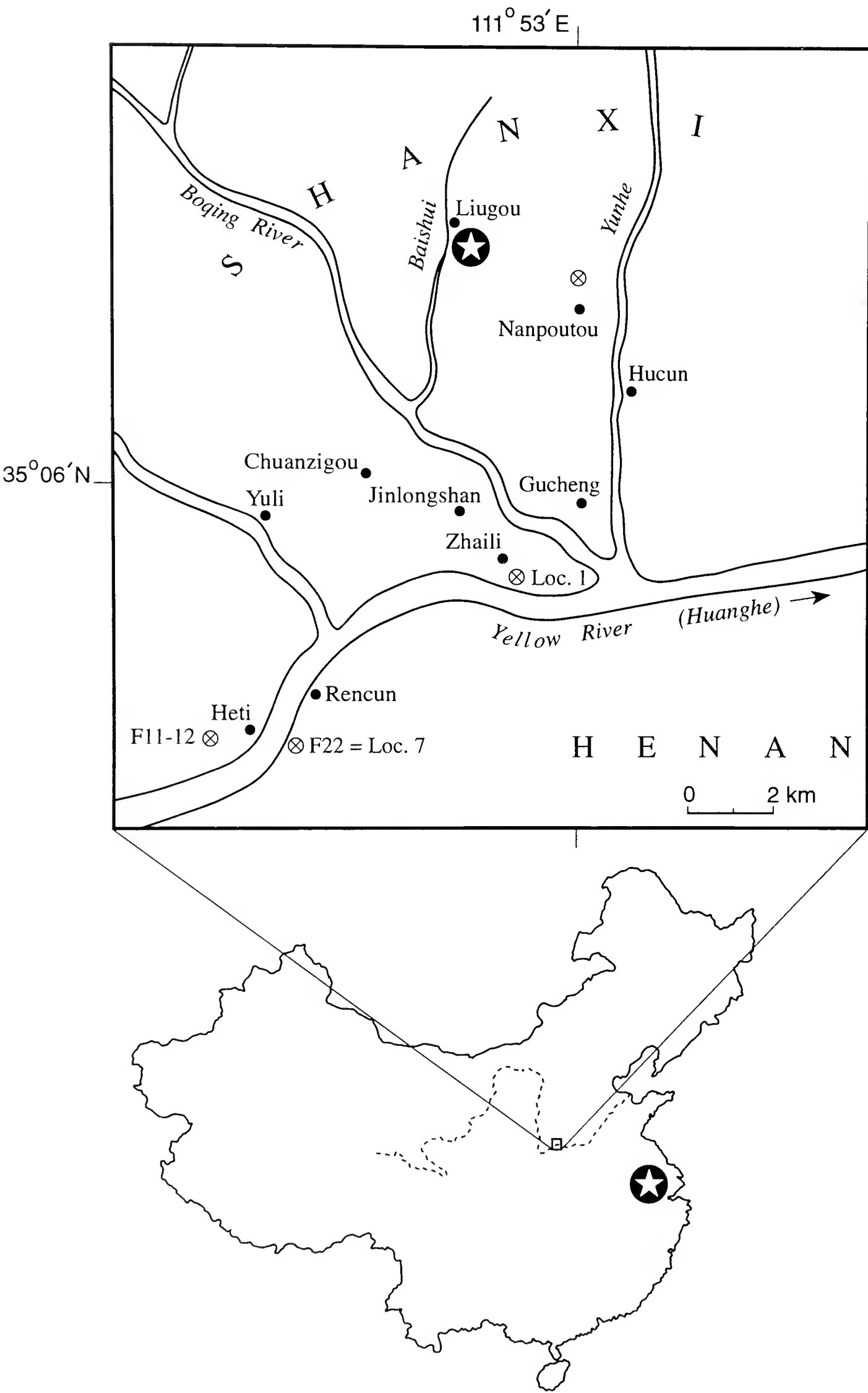
unknown whether *Xanthorhysis* possessed a single, relatively small, nearly vertically oriented lower incisor like that in modern *Tarsius*, or if it retained two lower incisors as did *Eosimias* and many omomyid taxa. The absence of any trace of a large, subhorizontal alveolus for I_1 at the front of the dentary demonstrates that a massively hypertrophied and procumbent I_1 did not characterize *Xanthorhysis*. Therefore, *Xanthorhysis* did not resemble such derived omomyids as *Trogolemur* and *Pseudotetonius* in lower incisor morphology.

Xanthorhysis differs from all omomyids, and resembles modern *Tarsius*, in having a large alveolus for C_1. Within Omomyidae, the largest C_1 alveoli or crowns are found in *Teilhardina belgica*, *Steinius vespertinus*, and *Dyseolemur pacificus* (Gingerich, 1977; Bown and Rose, 1987; Rose and Bown, 1991; Rasmussen et al., 1995), but no omomyid is known to have possessed a C_1 alveolus as large as those in *Tarsius* and *Xanthorhysis*. As occurs variably in extant *Tarsius*, the root for C_1 in *Xanthorhysis* was enlarged to the extent that the labial surface of the dentary is swollen in the vicinity of the C_1 alveolus. Similar swelling of the labial side of the dentary is never encountered in omomyids, even among specimens in which the C_1 alveolus is relatively large. While the large C_1 alveolus and associated labial swelling of the dentary distinguish *Xanthorhysis* and *Tarsius* from all omomyids, the polarity of this character complex is open to debate. In addition to its occurrence in certain omomyids, a relatively large C_1 is also found in many adapiforms, basal anthropoids, and the basal primate *Altanius*, suggesting that a relatively large C_1 may well have characterized all primitive primates (Rose and Bown, 1991; Rose et al., 1994). If so, its occurrence in *Xanthorhysis* and *Tarsius* cannot be used as an argument for their close relationship.

Problematic polarity issues do not pertain to P_{3-4} of *Xanthorhysis*, which show clearly derived features that are otherwise restricted to *Tarsius* among primates. On both P_{3-4} in *Xanthorhysis*, highly trenchant crests emanate from the protoconids, running mesially and distolingually toward the bases of

the crowns. Weaker crests run distolabially from the protoconids of these teeth, resulting in a subpyramidal shape for each protoconid. P_{3-4} in *Tarsius* resemble those of *Xanthorhysis* in remarkable detail, differing only in being relatively shorter mesiolingually, with roots much more closely appressed or variably fused. Although similarly positioned crests occur on P_{3-4} in many omomyids, these crests are never as trenchant as they are in *Xanthorhysis* and *Tarsius*, and the protoconids of P_{3-4} are more inflated and less pyramidal in shape as a result. *Tarsius* and *Xanthorhysis* further differ from all omomyids in having the apices of the protoconids of P_{3-4} curved linguad (especially apparent in distal view), which results from the strong labial convexity and lingual flatness or concavity of the protoconids in the former taxa.

The lower molars of *Xanthorhysis* notably lack several synapomorphies found in living and fossil species of *Tarsius*, including *T. eocaenus* from the Shanghuang fissure fillings. The crowns of M_{1-2} in *Xanthorhysis* are relatively longer and narrower than in *Tarsius*. These proportions of the lower molars of *Xanthorhysis* are likely to be primitive for tarsiiform primates, because *Xanthorhysis* is similar in this respect to such primitive omomyids as *Steinius vespertinus* (Fig. 3). *Tarsius thailandicus* from the middle Miocene and all living species of *Tarsius* uniformly have higher-crowned M_{1-3} than does *Xanthorhysis*, which resembles omomyids and other primitive primates in lower molar crown height. Lower molar crown height in middle Eocene *Tarsius eocaenus* appears to be similar to that in *Xanthorhysis*; the high-crowned lower molars characteristic of Neogene and Recent species of *Tarsius* may therefore be a synapomorphy linking all of these species to the exclusion of the Eocene forms. Finally, the entoconids of M_{1-3} in *Xanthorhysis* are more distal in position than is the case in living and fossil species of *Tarsius*, a feature that may be correlated with the relatively longer and narrower lower molars of *Xanthorhysis* compared with *Tarsius*. In this respect *Xanthorhysis* again resembles omomyids.

←

Fig. 2.—Map of the Yuanqu Basin showing geographic location of major primate-bearing fossil localities in the Eocene Heti Formation. The type locality for *Xanthorhysis tabrumi* (designated by a star in the detailed map) occurs in an ephemeral drainage that consitutes an eastern tributary to the larger Baishui drainage, south of Liugou village. Type localities for other Eocene primate taxa known from the Heti Formation are as follows: *Hoanghonius stehlini* and *Eosimias centennicus*, Locality 1 on the northern bank of the Yellow River, just southeast of Zhaili village; *Rencunius zhoui*, Locality 7 on the southern bank of the Yellow River, directly opposite Heti village. The geographic location of the Shanghuang fissure fillings, type locality for *Tarsius eocaenus*, is marked by a star near the eastern coast of China.
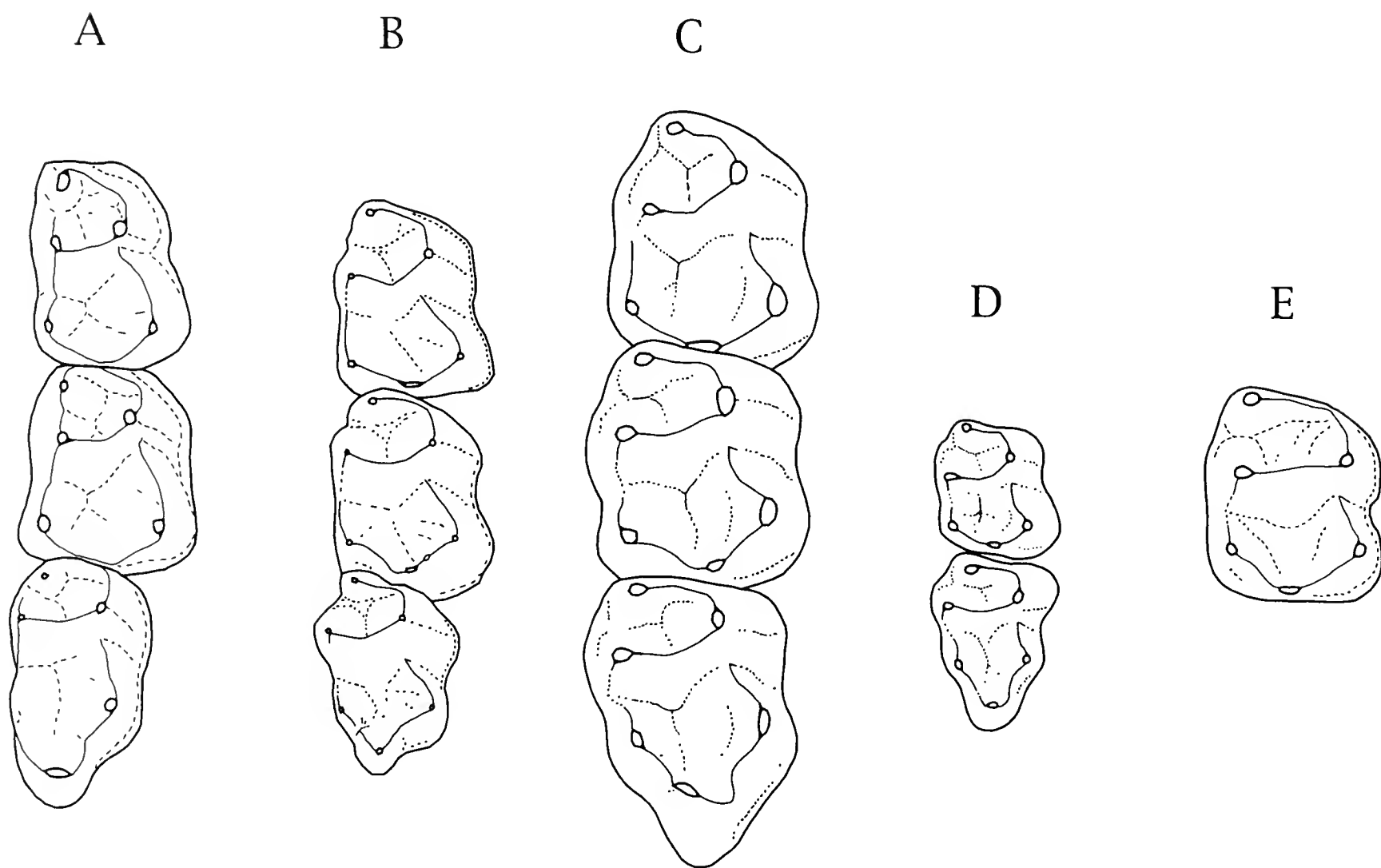
Fig. 3.—Comparative schematic drawings of the lower molar dentition in some living and fossil tarsiiform primates. Taxa depicted are as follows: A. *Steinius vespertinus*, B. *Xanthorhysis tabrumi* (reversed for comparative purposes), C. *Tarsius bancanus*, D. *Tarsius eocaenus*, E. *Tarsius thailandicus*. All schematic drawings are shown at the same scale.

Despite the fact that *Xanthorhysis* shares several apparently primitive lower molar traits in common with various omomyids, certain features of the lower molars of *Xanthorhysis* are unlike those of any omomyid. For example, the paraconid and metaconid are not closely connate on M_{2-3} in *Xanthorhysis*, as is invariably the case in omomyids. Interestingly, in this feature *Xanthorhysis* resembles not only *Tarsius*, but also certain basal anthropoids, including *Eosimias*. The protoconid and metaconid on M_{2-3} are also widely separated from one another in *Xanthorhysis*, whereas in omomyids these cusps are virtually always more closely spaced. In this respect *Xanthorhysis* lower molars again resemble those of both *Tarsius* and basal anthropoids such as *Eosimias*. Finally, the lower molar entoconids in *Xanthorhysis*, while similar in position to those of omomyids, are more strongly developed than in most omomyids (particularly primitive forms such as *Teilhardina*). Possibly correlated with this strong development of the molar entoconids in *Xanthorhysis*, the molar entocristids are more trenchant than in most omomyids. *Xanthorhysis* resembles *Tarsius* in this respect.

Reconstruction of the phylogenetic position of *Xanthorhysis tabrumi* is necessarily based on the limited anatomical evidence at hand, that is, on characters of the dentary and lower cheek teeth. Nevertheless, this evidence demonstrates that *Xanthorhysis* resembles *Tarsius* to the exclusion of other primates in several important ways, particularly in the morphology of the preserved lower premolars (P_{3-4}). That which remains of the front part of the dentary in *Xanthorhysis* is fully consistent with this region in *Tarsius* in having a large alveolus for C_1 and labial swelling of the dentary in the region of this alveolus. No omomyid recovered to date preserves both of these features, but the possibility remains that at least the relatively large size of the C_1 alveolus may be primitive for primates. Critically missing is information on the number of lower incisors and their mode of implantation, but the preserved part of the symphyseal region in *Xanthorhysis* is inconsistent with the presence of a hypertrophied, strongly procumbent I_1 as occurs in several omomyids. The lower molars are clearly more primitive than those of species of *Tarsius*, including *Tarsius eocaenus* and *Tarsius thailandicus*. On the

other hand, details of the placement of molar trigonid cusps and the relatively strong molar entoconids and trenchant entocristids in *Xanthorhysis* may represent derived characters shared with *Tarsius* to the exclusion of omomyids. The presence of similar lower molar trigonid characters in *Eosimias*, *Xanthorhysis*, and *Tarsius* is an interesting means by which these taxa differ from omomyids, but these features are here considered to be an insufficient basis for positing a phylogenetic relationship between early anthropoids and tarsiids exclusive of the Omomyidae. Cranial and postcranial data sets must also be considered in phylogenetic reconstructions of haplorhine primates, but these data are largely missing for such critical fossil taxa as *Eosimias* and *Xanthorhysis*.

In an attempt to evaluate the phylogenetic position of *Xanthorhysis* as rigorously as possible, dental and gnathic characters having potential phylogenetic significance were identified and coded in this taxon, other living and fossil species of Tarsiidae, the representative omomyids *Teilhardina belgica*, *Steinius vespertinus*, and *Shoshonius cooperi*, and the basal adapiform *Cantius* (Appendices 1, 2). Selected characters of the pelage, cranial skeleton, and postcranial skeleton were also incorporated into the data set, although these features are largely unknown for the fossil forms. Parsimony analysis of these data using the branch-and-bound algorithm in PAUP 3.1.1 (Swofford, 1993) yielded nine most parsimonious trees (MPTs), a strict consensus of which is illustrated in Figure 4.

Certain nodes in Figure 4 are strongly supported by character transformations, while other relationships must be considered more tenuous. Significantly, the sister-group relationship between *Xanthorhysis tabrumi* and the clade including all living and fossil species of *Tarsius* is the most highly corroborated node depicted in Figure 4, being supported by eight unambiguous synapomorphies. Character support for the clade including all tarsiiforms (or all haplorhines, since anthropoids were excluded from this analysis) is also relatively strong, being corroborated by three unambiguous synapomorphies. Support for the monophyly of all living and fossil species of *Tarsius* is based on two unambiguous synapomorphies, a surprisingly robust result given that both fossil species of *Tarsius* are known only by isolated cheek teeth. Weakly supported by this analysis are the nodes uniting *Shoshonius* + Tarsiidae (one unambiguous synapomorphy) and *Tarsius thailandicus* + the extant species of *Tarsius* (one unambiguous synapomorphy). Seven of the nine MPTs generated by this analysis recognize a sister-group relationship between Sundanese *Tarsius bancanus* and *Tarsius syrichta* from the southern Philippines, in agreement with most previous workers (e.g., Musser and Dagosto, 1987). Two MPTs did not support a strict *Tarsius bancanus* + *Tarsius syrichta* clade because the poorly known fossil species *Tarsius thailandicus* formed an unresolved polytomy with them, but this result may be due to missing data for *Tarsius thailandicus*.

IMPLICATIONS FOR HIGHER-LEVEL PRIMATE PHYLOGENY

Many studies of tarsiiform phylogeny have suggested that the diverse array of early Tertiary forms commonly grouped within Omomyidae constitutes a paraphyletic stem lineage for Tarsiidae (e.g., Szalay, 1976; Hoffstetter, 1977; Gingerich, 1981; Rosenberger, 1985; Beard et al., 1991; Beard and MacPhee, 1994). If so, certain omomyids share more recent common ancestry with Tarsiidae than they do with one another. While this model of tarsiid origins may well prove to be true, it is surprising that *Xanthorhysis* lacks the clear resemblances to particular clades of omomyids needed to bolster the hypothesis of omomyid paraphyly. Alternatively, the absence of conspicuous dental and gnathic synapomorphies between early tarsiids and particular omomyid clades may imply that Omomyidae is monophyletic after all, and that tarsiids and omomyids diverged from a common tarsiiform ancestor

very early in the Cenozoic (before the basal Wasatchian/Sparnacian). However, this interpretation conflicts with the cranial evidence suggesting that certain omomyids are more closely related to Tarsiidae than to one another, and synapomorphies linking all omomyids to the exclusion of tarsiids are equally elusive. Teasing apart the basal radiation of fossil tarsiiforms will require broader sampling of cranial anatomy among omomyid clades (cf. Beard and MacPhee, 1994), as well as the recovery of more nearly complete fossil tarsiids than are currently available.

As noted above and by many workers on omomyid phylogeny (e.g., Bown and Rose, 1987), the morphology of the lower premolars is often a critical character complex for reconstructing early tarsiiform phylogeny. It is therefore significant that the lower premolars of *Xanthorhysis* retain several
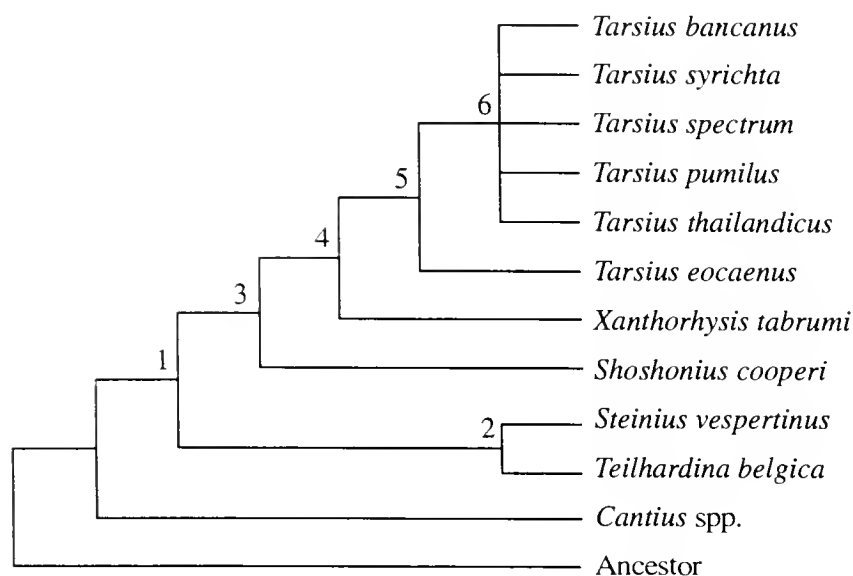
Fig. 4.—Strict consensus of nine MPTs yielded by branch-and-bound search in PAUP 3.1.1 (Swofford, 1993) of mostly dental and gnathic characters (see Appendices 1, 2). Tree was rooted by designating *Cantius* spp. and "Ancestor" as outgroups to remaining taxa. Tree length = 24; consistency index = 0.958.

Using the ACCTRAN character state optimization algorithm in PAUP, character transformations supporting each node are as follows (see Appendix 1 for description of character states): Node 1 (Tarsiiformes or Haplorhini), Character 4 (0→1), Character 5 (0→1), Character 6 (0→1); Node 2, Character 1 (0→1); Node 3, Character 4 (1→2); Node 4 (Tarsiidae), Character 1 (0→2), Character 2 (0→1), Character 3 (0→1), Character 8 (0→1), Character 9 (0→1), Character 11 (0→1), Character 12 (0→1), Character 15 (0→1), Character 16 (0→1); Node 5 (*Tarsius*), Character 7 (0→1), Character 10 (0→1), Character 13 (0→1); Node 6, Character 14 (0→1).

primitive character states that are frequently transformed in various omomyid clades. For example, neither P_3 nor P_4 shows significant mesiodistal compression (in contrast to many advanced anaptomorphines, washakiins, and microchoerines), P_3 lacks a metaconid (in contrast to many advanced anaptomorphines and washakiins) and shows no reduction in crown height (in contrast to many anaptomorphines and microchoerines), P_4 lacks a distinct paraconid and possesses a metaconid that is situated

low on the trigonid (in contrast to many anaptomorphines, all washakiins, *Macrotarsius*, and *Hemiacodon*) and is not hypertrophied (in contrast to *Absarokius*, *Tetonius*, *Uintanius*, *Anaptomorphus*, and other taxa). Indeed, only the most primitive known omomyids, such as *Teilhardina belgica* and *Steinius vespertinus*, possess sufficiently primitive P_{3-4} to have been ancestral to *Xanthorhysis* without postulating significant character state reversals in lower premolar morphology among early Tarsiidae. It therefore seems likely that cladogenesis between Tarsiidae and whichever omomyid clade comprised its sister group occurred very early—probably by the early part of the early Eocene, if not earlier.

If *Xanthorhysis tabrumi* and *Tarsius eocaenus* are accurately interpreted as early tarsiids, their anatomy and age add further data to the ongoing debate regarding anthropoid origins and tarsiid relationships. First, for workers who consider *Tarsius* to be the closest living relative of anthropoids, the middle Eocene age of *Xanthorhysis* and *T. eocaenus* requires an origin for the anthropoid clade of at least this antiquity. As such, these Eocene tarsiids corroborate conclusions reached in a similar manner on the basis of the cranial anatomy of the omomyid *Shoshonius* (Beard et al., 1991; Beard and MacPhee, 1994). However, because some workers continue to see merit in a strict Tarsiidae + Anthropoidea clade (exclusive of omomyids such as *Shoshonius*), the antiquity of *Xanthorhysis* and *T. eocaenus* is important in requiring all advocates of haplorhine monophyly to support a relatively ancient divergence of anthropoids from other living primate clades. At the same time, the distinctly tarsier-like anatomy now known for *Xanthorhysis* conflicts with Cartmill's (1980:261) prediction that ". . . in some respects the last common ancestor of *Tarsius* and anthropoids was more like a small monkey than a modern tarsier . . . ."

VICARIANCE, DISPERSAL, AND THE HISTORICAL BIOGEOGRAPHY OF TARSIERS

The geographic distribution of living tarsiers is unusual in several respects (Fig. 5), and these distributional patterns pose interesting puzzles for historical biogeographers. First, given that tarsiiform primates were both widespread and diverse on Holarctic continents during the Eocene (e.g., Szalay, 1976; Russell and Gingerich, 1980, 1987; Beard, 1987; Bown and Rose, 1987, 1991; Beard and Wang, 1991; Beard et al., 1992, 1994; Godinot et al., 1992; Williams and Covert, 1994; Gunnell,

1995; Rose, 1995; Rasmussen, 1996), why are living tarsiers restricted to offshore islands in southeastern Asia? Second, how can we account for the fact that tarsiers are among the few placental mammal taxa to be distributed on both sides of "Wallace's Line" (Musser, 1987; Musser and Dagosto, 1987), which consists in part of the deep waters of the Makassar Strait separating Sulawesi and Borneo?

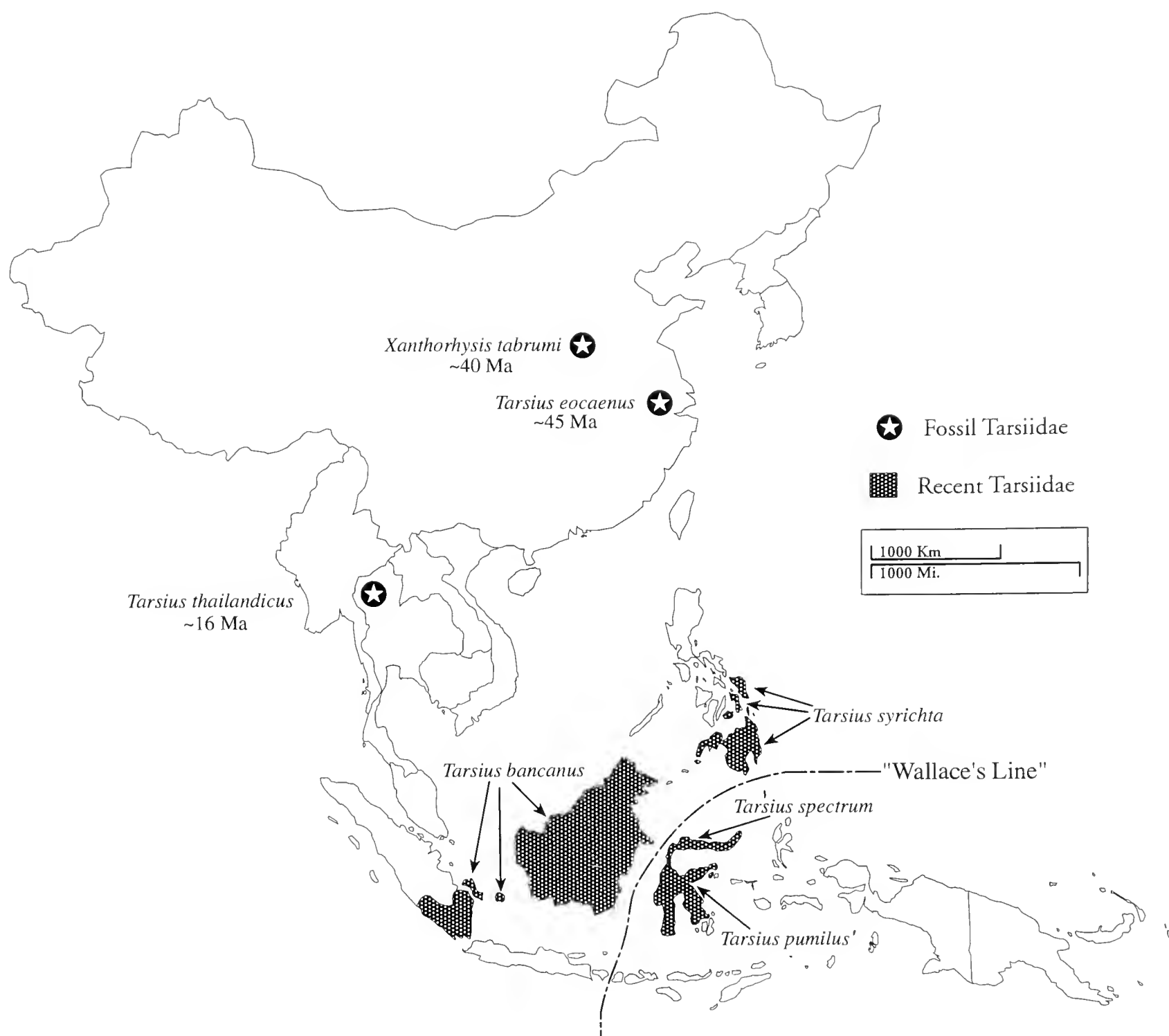The modern range restriction of tarsiers to south-

Fig. 5.—Map of eastern and southeastern Asia showing geographic distribution of living and fossil Tarsiidae. Undoubted fossil tarsiids are unknown outside of the area depicted here.

eastern Asian islands may be explicable on the basis of paleogeographic and paleoclimatic reconstructions. During the middle Eocene climatic conditions were sufficiently warm and moist to support a diversity of tarsiiform primates at relatively high latitudes throughout the Northern Hemisphere. In North America both omomyine (*Omomys*, *Macrotarsius*) and anaptomorphine (*Trogolemur*) omomyids are known from Uintan and Duchesnean localities as far north as Saskatchewan (Storer, 1984, 1990). In the middle Eocene of Europe, microchoerine omomyids are represented in localities as far north as the Hampshire Basin of southern England (Hooker, 1986) and Geiseltal in central Germany (e.g., Franzen and Haubold, 1986). To date, middle

Eocene tarsiiform primates have proven to be much less common in the Asian fossil record. However, both omomyids (*Macrotarsius*, *Asiomomys*) and tarsiids (*Xanthorhysis*, *Tarsius eocaenus*) are now recorded from the Asian mainland during this interval (Beard and Wang, 1991; Beard et al., 1994; also see Fig. 5). Relatively high-latitude Asian occurrences are documented for the omomyid *Asiomomys* (Jilin Province, northeastern China) and the tarsiid *Xanthorhysis* (Shanxi Province, central China) in the middle Eocene of Asia.

This widespread, Holarctic distribution of tarsiiform primates in the middle Eocene coincided with optimally warm, equable, and subtropical conditions on a global scale for the Cenozoic Era (e.g.,
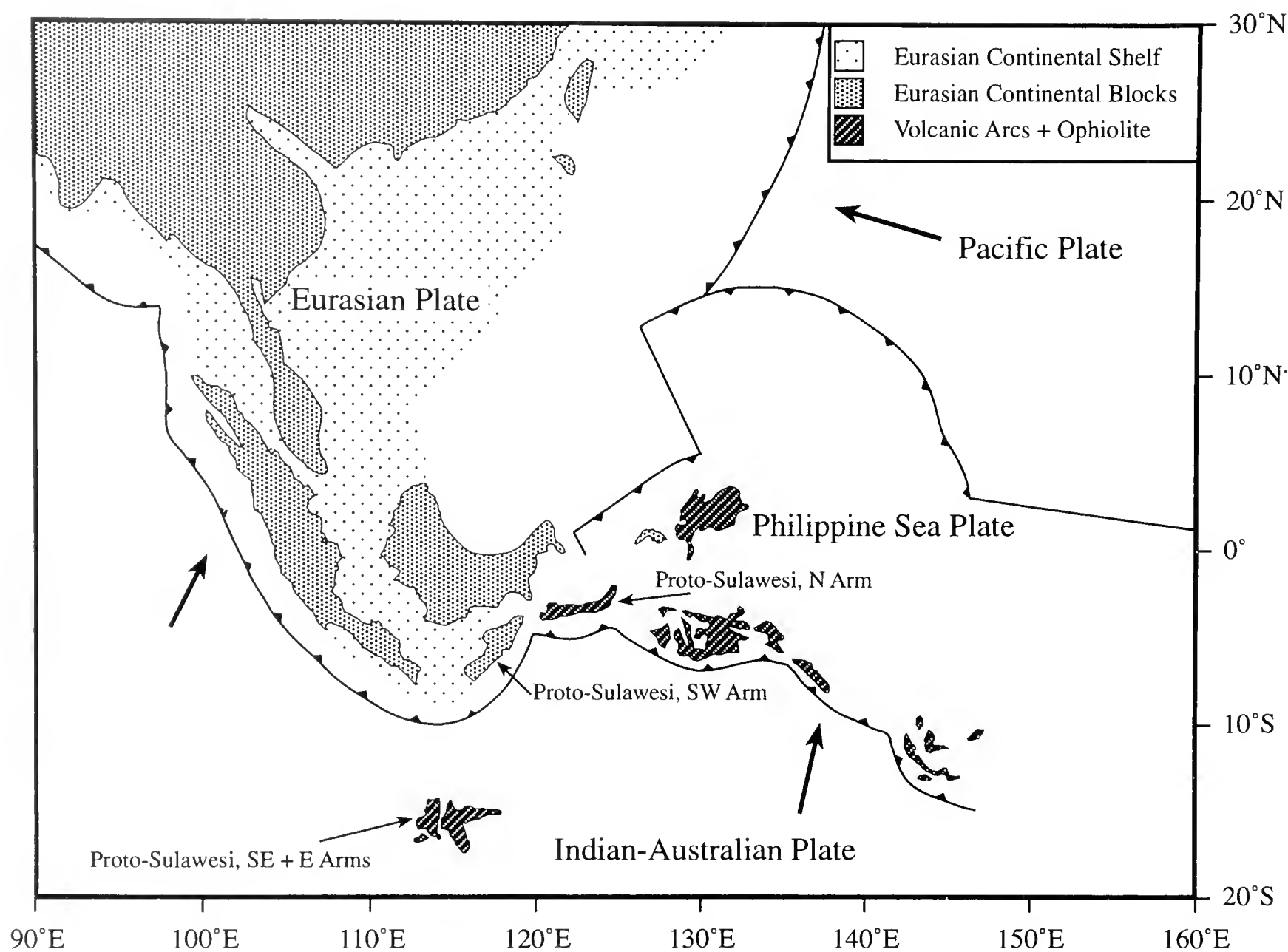
Fig. 6.—Paleogeographic reconstruction of southeastern Asia at 40 Ma, modified after Hall (1996:fig.9). Note that rifting between the continental block that will ultimately become the southwestern arm of Sulawesi and the remainder of the Eurasian plate was not completed at this time. Also note the allochthonous origin of terranes comprising the remainder of Sulawesi.

Wing, 1987; Prothero and Berggren, 1992; Prothero, 1994). However, near the middle/late Eocene boundary these greenhouse conditions began progressively to deteriorate. Rather dramatic cooling, associated with increased aridity in continental interiors, is documented during the interval between the middle Eocene and early Oligocene by several lines of evidence. These data include changes in stable oxygen isotopes derived from benthic foraminifera (Miller, 1992), taxonomic turnover in planktonic foraminifera (Keller et al., 1992) and calcareous nannoplankton (Aubry, 1992), changes in geochemical characteristics of paleosols (Retallack, 1992), and changes in the taxonomic composition of terrestrial floras (Wing, 1987; Collinson, 1992) and faunas (Hooker, 1992; Hutchison, 1992; Stucky; 1992). Climatic cooling and drying during the middle Cenozoic, along with associated vegetational changes, undoubtedly affected the geographic distribution of Paleogene primates. Indeed,

middle Cenozoic primate distributions were impacted on a continental scale, because primates apparently became extinct by early Oligocene time in both Europe and North America (cf. Beard and Dawson, 1994). In contrast, Asian tarsiiforms seemingly endured the middle Cenozoic climatic deterioration that decimated their North American and European relatives.

Paleogeographic reconstructions of continental configurations near the Eocene–Oligocene boundary suggest that this differential extinction of tarsiiform primates on Holarctic continents may have been determined by the accessibility of low latitude refugia as middle Cenozoic climatic deterioration progressed. Throughout the Cenozoic, Asia maintained a vital geographic link to the tropics, because the present islands of the Sunda Shelf occur on the extreme southeastern margin of the Eurasian Plate (Fig. 6; Smith et al., 1994; Hall, 1996). Terranes such as those comprising the modern islands of Su-

matra and Borneo have been positioned at or near 0° latitude over the course of the entire Cenozoic (Hall, 1996). Direct (i.e., subaerial) geographic contiguity between these Sundanese islands and the Asian mainland was probably intermittent throughout the Cenozoic, varying largely as a function of eustatic sea level. Near the Eocene–Oligocene boundary, climatic cooling and the onset of Antarctic glaciation resulted in a glacioeustatic lowering of sea levels of at least 30 m (Miller, 1992), which would have broadened subaerial connections between the Asian mainland and emergent parts of the Sunda Shelf. At some point during the Cenozoic (possibly as early as the Eocene), tarsiids were able to exploit these geographic links between the Sunda Shelf and the Asian mainland. Indeed, it seems highly likely that the survival of tarsiids to the present was fostered by their access to the Sunda Shelf and its environs, which allowed them to weather the middle Cenozoic climatic deterioration in a contracted, low latitude refugium.

In contrast to Asia, neither Europe nor North America offered such reliable and sustained access to low latitude refugia during the middle Cenozoic interval of climatic deterioration. Unless European tarsiiforms were able to disperse across the western Tethys to North Africa (and there is no evidence that they ever did so; see below), middle Cenozoic tarsiiforms in Europe would have been unable to retreat to latitudes lower than about 30°N, which would have corresponded to the southernmost extent of the Iberian Peninsula at that time (Smith et al., 1994). Access to lower latitude regions should have been more feasible in North America, despite the fact that no direct geographic connection to the South American tropics existed during the middle Cenozoic. The paleogeographic reconstructions of southern North America near the Eocene–Oligocene boundary published by Smith et al. (1994:maps 5, 6) show emergent land as far south as about 10°N latitude, in the vicinity of what is now southern Mexico. While this geographic configuration would have been more favorable than that of Europe for providing a low latitude refugium for middle Cenozoic tarsiiforms, the youngest known North American tarsiiforms are Chadronian (latest Eocene) in age (Ostrander, 1987). Unfortunately, the Paleogene fossil record of Mexico (see Fries et al., 1955; Black and Stephens, 1973; Ferrusquia-Villafranca, 1989; Novacek et al., 1991) is insufficient to assess whether or not southernmost North America harbored tarsiiforms and other faunal elements be-

yond the time of their disappearance in the fossil record of the United States.

The only records of undoubted tarsiiforms from terranes of Gondwanan origin are isolated teeth and a right dentary preserving P_4 from the late early Eocene Kuldana Formation of Pakistan. All of these specimens have been attributed to the omomyid *Kohatius* (Russell and Gingerich, 1980, 1987). Because these Kuldana Formation omomyids probably postdate the India–Asia collision (Beck et al., 1995; McKenna, 1995; Rage and Jaeger, 1995), they are irrelevant for inferring any earlier or geographically more widespread Gondwanan distribution of tarsiiforms. In particular, there is no compelling evidence that tarsiiforms ever inhabited the Afro–Arabian continent. Assertions to the contrary have been based on two poorly known fossil taxa, *Afrotarsius chatrathi* (Simons and Bown, 1985) and *Altiatlasius koulchii* (Sigé et al., 1990), and isolated teeth attributed to unnamed tarsiiforms or omomyids from the Jebel Qatrani Formation, Fayum region of Egypt (Simons et al., 1986) and the Ashawq Formation, Dhofar Province, Oman (Thomas et al., 1988, 1989). Each of these alleged tarsiiform records will be briefly discussed here, to illustrate why they constitute inadequate evidence for inferring a geographic range extension of tarsiiforms to Afro–Arabia.

Afrotarsius chatrathi is known from a single right dentary fragment preserving $M_{1–3}$ and the bases of the crowns of $P_{3–4}$. Although this species was originally described as a possible tarsiid (Simons and Bown, 1985; also see Simons et al., 1986, 1995), several subsequent workers have noted features that may indicate anthropoid affinities for this taxon (Fleagle and Kay, 1987; Ginsburg and Mein, 1987; Kay and Williams, 1994; Van Valen, 1994; Kay et al., 1997). Obviously, the fragmentary material currently available for *Afrotarsius* severely limits the degree of confidence one can place in any phylogenetic reconstruction for this taxon. Nevertheless, several characters do favor anthropoid affinities for this small primate, and *Afrotarsius* is tentatively considered to be a basal anthropoid here. The most important derived characters for inferring anthropoid affinities for *Afrotarsius* include: 1) apparent oblique orientation of P_4 (as occurs in *Eosimias* and most other basal anthropoids); 2) apparent large size of molar protoconids relative to metaconids (because all of the lower molar trigonids on the single specimen of *Afrotarsius* are somewhat damaged, the occurrence of this character state in *Afrotarsius* is not entirely certain); and 3) reduced hypoconulid lobe on M_3 (as occurs in *Eosimias* and other basal

anthropoids; cf. Ginsburg and Mein, 1987). Although I tentatively consider *Afrotarsius* to be a basal anthropoid, it is certainly premature to synonymize the family Afrotarsiidae Ginsburg and Mein, 1987 with the family Eosimiidae Beard et al., 1994 as Van Valen (1994) and Kay et al. (1997) suggested.

Altiatlasius koulchii is a very primitive primate represented by roughly ten isolated teeth from the late Paleocene Adrar Mgorn 1 locality, Ouarzazate Basin, Morocco (Sigé et al., 1990). Although this taxon remains poorly known anatomically, its phylogenetic and biogeographic significance is considerable because of its great antiquity. Indeed, *Altiatlasius* is the oldest primate currently documented in the fossil record (Sigé et al., 1990; see also Godinot, 1994; Rose et al., 1994). Although Sigé et al. (1990) originally classified *Altiatlasius* as an omomyid tarsiiform, its potential affinities with basal anthropoids were recognized at that time. Godinot (1994) cited further characters suggesting anthropoid affinities for *Altiatlasius*, and this conclusion is tentatively accepted here. Interesting dental similarities between *Altiatlasius* and *Eosimias* are evident, including paraconid and metaconid being widely separated on M_2 and molar entoconids being relatively anterior in position.

The isolated premolars from the Fayum, Egypt, described as omomyids by Simons et al. (1986) cannot be considered reliable records of this family. Rather, from the published illustrations, it appears that the isolated left P_4 (DPC 5403) would have been obliquely oriented in the lower jaw, as is the case in *Eosimias* and other basal anthropoids. This possibility can be verified by inspecting the root configuration of this specimen, which is not observable in the published illustration (Simons et al., 1986:fig. 1a). In isolated P_4s of eosimiids and other basal anthropoids, the mesial root is situated labial of the midline and the distal root is situated lingual of the midline, a condition that results in the oblique orientation of the premolar in the toothrow. Similarly, the isolated left P^4 (DPC 2809) assigned by Simons et al. (1986) to the Omomyidae possesses a protocone that is more labial in position than in undoubted omomyids (this was noted by Simons et al., [1986:433] who called the "internally situated" protocone of P^4 "unique"). A similar position of the P^4 protocone occurs in eosimiids (undescribed specimens) and many other basal anthropoids, including platyrrhines. In light of these considerations, I regard the isolated premolars referred by

Simons et al. (1986) to the Omomyidae as belonging to an indeterminate basal anthropoid.

Two isolated molars from the early Oligocene Ashawq Formation, Oman, were described as possible omomyids by Thomas et al. (1988, 1989). Recovery of additional specimens from this rock unit led Gheerbrant et al. (1995) to refer these specimens to the Oligopithecinae.

To summarize, all of the alleged records of tarsiiform primates from the Paleogene of the Afro–Arabian continent are more likely to pertain to various basal anthropoid taxa. Although the Afro–Arabian Paleogene record is still only poorly sampled, indisputable tarsiiforms have yet to be recorded from this landmass. Hence, tarsiiform primates may well have been restricted to Holarctic continents throughout their evolutionary history. Indeed, if the paleogeographic and paleoclimatic model accounting for the differential extinction of tarsiiforms on Holarctic continents outlined above is broadly correct, it would be difficult to explain why tarsiiforms are not part of the extant fauna of equatorial Africa if they ever inhabited this landmass.

As noted above, the modern geographic restriction of Tarsiidae to Sulawesi, the southern Philippines, and islands of the Sunda Shelf is clearly a relictual distribution (Fig. 5). Most of the contraction in the geographic range of Asian tarsiids probably occurred in response to middle Cenozoic climatic deterioration, which coincided with tarsiiform extinction on North America and Europe, where low latitude refugia were not then accessible. Interestingly, later Tertiary tarsiids were not restricted to offshore islands of southeastern Asia, as middle Miocene *Tarsius thailandicus* from northern Thailand attests. The extirpation of tarsiids on the Asian mainland therefore postdates middle Cenozoic climatic deterioration, but the fossil record of Neogene tarsiids is insufficient to determine further details regarding the timing or cause of their demise on the Asian mainland.

Although the fossil record of the southeastern Asian islands comprising the current range of *Tarsius* is poor indeed, a geographic origin for the family Tarsiidae on the Asian mainland is advocated here. The earliest known records of the family, *Xanthorhysis tabrumi* and *Tarsius eocaenus*, occur in the middle Eocene of China. Of these, *Xanthorhysis tabrumi* in particular retains primitive characters that suggest this species lies outside the clade containing all living and fossil species of *Tarsius*. More distant outgroups, in the form of the omomyids *Macrotarsius macrorhysis*, *Asiomomys changbaicus*,

and *Kohatius coppensi*, are also known from the Asian mainland. If tarsiers did originate on the Asian mainland as their Tertiary fossil record suggests, the hypothesis of Groves (1976) and Niemitz (1984c) that tarsiers may have originated on Sulawesi can finally be abandoned. The latter possibility, based on the retention of primitive character states in the Sulawesian species *Tarsius spectrum* and *T. pumilus* as opposed to the Philippine species *T. syrichta* and the Sundanese species *T. bancanus*, has been criticized previously on the basis of comparisons with the distributional patterns of other mammalian taxa (Musser, 1987; Musser and Dagosto, 1987).

If the assertion that tarsiers originated on the Asian mainland, or at least somewhere other than Sulawesi, is correct, it remains to be explained how tarsiers were able to cross "Wallace's Line" and occupy the latter island. Most recent authors have advocated overwater dispersal from the nearby islands of the Sunda Shelf, especially Borneo, in explaining the origin of the placental land mammals of Sulawesi (Cranbrook, 1981; Musser, 1987). The depauperate and unbalanced taxonomic composition of the land mammal fauna of Sulawesi compared with that of Borneo is certainly consistent with this interpretation. Yet the great antiquity of tarsiids now demonstrated by their fossil record makes an alternative biogeographical hypothesis for the origin of Sulawesi's tarsiers more plausible than earlier workers could have conceived.

The geological origin of Sulawesi itself is highly complex because the island lies in a tectonically active region near the juncture of several of the Earth's major plates (Fig. 6; Hamilton, 1979; Bergman et al., 1996; Hall, 1996; Wilson and Bosence, 1996). What is now the southwestern arm of Sulawesi originally formed the southeasternmost margin of the Sunda Shelf (Fig. 6; Hamilton, 1979; Hall, 1996). Obduction of the ophiolitic terranes comprising what are today the southeastern and eastern arms of Sulawesi onto the continental core of the island occurred at the end of the Oligocene (Hall, 1996, and references cited therein). The northern arm of Sulawesi originated as part of an island arc formed by subduction of the Indian–Australian Plate beneath the Philippine Sea Plate in the middle Eocene (Fig. 6; Hall, 1996:fig. 9, 10), but this terrane was not accreted onto the core of Sulawesi until the later Neogene. Multiple Neogene collisions

with continental fragments deriving ultimately from the Australian Plate complete the tectonic picture as it is currently understood (Bergman et al., 1996; Hall, 1996).

For the purpose of understanding how tarsiers came to lie on either side of "Wallace's Line," it is potentially highly significant that the southwestern arm of Sulawesi formed the southeastern margin of the Sunda Shelf in the early Tertiary (Fig. 6). Wilson and Bosence (1996:378) present geological data showing that at least parts of the southwestern arm of Sulawesi were emergent as early as the late Eocene. Rifting between western Sulawesi and eastern Borneo, forming the present Makassar Strait, probably occurred in the middle Paleogene (ca. 44–34 Ma), although timing is poorly constrained (Hall, 1996). Alternatively, Bergman et al. (1996) propose that the Makassar Strait formed as a foreland basin that resulted from the Miocene collision between Sulawesi and terranes deriving ultimately from the northern part of the Australian Plate. In either case, if *Tarsius* occupied the Sunda Shelf in the Paleogene, which is plausible given the middle Eocene age and very modern appearance of teeth attributed to *Tarsius eocaenus* (Beard et al., 1994), it is possible that tarsiers arrived on Sulawesi by means of vicariance rather than overwater dispersal. This possibility of an ancient (i.e., Paleogene) dichotomy between Sulawesian tarsiers and the *T. syrichta* + *T. bancanus* clade is consistent with the retention of primitive morphological character states in the former, as enunciated by Niemitz (1977) and Musser and Dagosto (1987). On the other hand, if tarsiers did reach Sulawesi by means of vicariance, it is difficult to explain why other Sundaic mammal clades of equivalent antiquity (e.g., Tupaiidae, Galeopithecidae) are not present on Sulawesi today (cf. Musser, 1987).

Determining whether tarsiers crossed "Wallace's Line" by means of overwater dispersal or vicariance is impossible given current knowledge of the fossil record of this region. Perhaps future paleontological exploration in this biogeographically fascinating part of the world will yield further clues. Additional neontological studies of the living species of *Tarsius*, particularly molecular phylogenetic studies, may also help to determine the antiquity of the dichotomy between tarsiers living east and west of "Wallace's Line."

ACKNOWLEDGMENTS

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APPENDIX 1

Character Descriptions

The following characters formed the basis for the phylogenetic analysis depicted in Figure 5. Most characters were polarized on the basis of conditions present in the outgroup taxon *Donrussellia*. Certain characters (primarily soft tissue characters known only in living species of *Tarsius*) could not be polarized in this fashion. In these cases, the ancestral condition is coded as "?" in the hypothetical outgroup taxon "Ancestor" in Appendix 2. With the exception of character 4, multistate characters are treated as unordered for the purposes of parsimony analysis. Character 4, which comprises a logical morphocline, was treated as ordered.

1. $I_1 < I_2$ (0); $I_1 > I_2$ (1); single lower incisor (2).
2. C_1 alveolus larger than P_2 alveolus (0); C_1 alveolus much larger than P_2 alveolus (1).
3. Dentary unexpanded labially around C_1 alveolus (0); expanded (1).
4. P_1 present and unreduced (0); variably present or vestigial (1); absent (2).
5. P_2 double rooted (0); single rooted (1).
6. P_{3-4} narrow and elongate (0); shorter and wider (1).
7. P_3 double rooted with roots widely splayed (0); P_3 single rooted or roots closely appressed (1).
8. P_3 with weak crests mesially and distolingually, crown basally inflated (0); P_3 with very trenchant crests mesially and distolingually, crown subpyramidal in shape (1).
9. P_4 with weak crests mesially and distolingually, crown basally inflated (0); P_4 with very trenchant crests mesially and distolingually (1).
10. M_{1-2} long and narrow in occlusal outline (0); M_{1-2} shorter and wider in occlusal outline (1).
11. Entocristids on M_{1-3} weak (0); high and trenchant (1).
12. Entoconid on M_3 weak (0); strong (1).
13. M_{1-2} entoconids situated at distolingual margins of talonid basins (0); more mesial in position, nearer the metaconid (1).
14. Lower molar crown height moderate (0); high crowned (1).
15. M_3 hypoconulid lobe elongate, broad, and joined to entoconid by a crest (0); elongate, narrow, and not joined directly to entoconid by a crest (1); M_3 hypoconulid lobe reduced both mesiodistally and buccolingually (2).
16. M_{2-3} paraconid and metaconid closely connate (0); widely splayed (1).
17. Pelage consisting of darker, longer fur (0); pelage lighter in color, shorter (1).
18. Postauricular spot absent (0); present (1).
19. Presence of "scales" on ventral surface of tail (0); scales absent, replaced by patch of friction skin (1).
20. Nasals extend anteriorly to level of premaxilla (0); nasals retracted with respect to premaxilla (1).
21. Manual proportions with respect to body length as in *T. spectrum* (0); manus elongated with respect to condition in *T. spectrum* (1).

APPENDIX 2

Taxon-Character Matrix Used in Parsimony Analysis

Ancestor	00000	00000	00000	0??0	?
Cantius spp.	01000	00000	00000	0????	?
Teilhardina belgica	10011	10000	00000	0????	?
Steinius vespertinus	10011	10000	00000	0????	?
Shoshonius cooperi	00021	10000	00000	0??0	?
Xanthorhysis tabrumi	?1121	10110	11001	1????	?

Tarsius eocaenus	?????	????1	11101	1????	?
Tarsius thailandicus	?????	????1	1?11?	1????	?
Tarsius pumilus	21121	11111	11111	10100	0
Tarsius spectrum	21121	11111	11111	10100	0
Tarsius syrichta	21121	11111	11111	11011	1
Tarsius bancanus	21121	11111	11111	11011	1

NEW MATERIAL OF *PAPPOCRICETODON SCHAUBI*, AN EOCENE RODENT (MAMMALIA: CRICETIDAE) FROM THE YUANQU BASIN, SHANXI PROVINCE, CHINA

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ABSTRACT

Newly discovered fossils from the type locality of *Pappocricetodon schaubi* show that this primitive cricetid has an hystricomorphous skull with large infraorbital foramen, posterior edge of incisive foramen anterior to M^1, and P^4 absent. Reexamination of the three species referred to *Pappocricetodon* suggests that development of the family was well underway in Asia during the middle Eocene, and that *P. antiquus* may represent a separate lineage.

INTRODUCTION

Zdansky (1930) described the first Eocene cricetid rodent, *Cricetodon schaubi*, based on a right M$_2$ and a left M$_3$ from the "River Section" (Locality 1) in the Yuanqu Basin of southern Shanxi Province, China. The type locality is in Tuqiaogou, a valley near Zhaili village. He compared the Yuanqu species to the European Miocene species *Cricetodon gregarium* Schaub, 1925, and the Oligocene species *C. dubium* Schaub, 1925. These two European species were later widely separated taxonomically, for when the genus *Cricetodon* was reviewed by Fahlbusch (1964) and Thaler (1966), the species *C. gregarium* was referred to a new genus, *Democricetodon* Fahlbusch, 1964, and *C. dubium* to a new subgenus of *Cricetodon*, *Eucricetodon* Thaler, 1966.

In a subsequent study of the Oligocene cricetids of western Europe, Vianey-Liaud (1972) considered the Yuanqu species to be referable to *Eucricetodon* and closer to middle Oligocene species such as *E. huberi* than to *D. gregarium*. Lindsay (1977) re-garded Zdansky's material of the Yuanqu species as indeterminate at the generic level. Another specimen from the River Section, a left mandible with incisor and M$_1$, was identified questionably by Zdansky (1930) as a leptictid but was later referred to the Zapodidae, as ?*Parasminthus* sp. (reviewed in Vianey-Liaud, 1985). Now all of these Yuanqu specimens have been confirmed to be cricetids, and were allocated by Tong (1992) to his new Eocene genus *Pappocricetodon*.

In 1994 and 1995, paleontologists from the Carnegie Museum of Natural History and the Institute of Vertebrate Paleontology and Paleoanthropology collected additional mandibles and maxillae of *Pappocricetodon schaubi* from its type locality, the River Section. This material, described here, provides new morphological and phylogenetic information on Asian Eocene cricetids.

Abbreviations used in text are: IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; PIU, Paleontological Institute, Uppsala, Sweden.

SYSTEMATIC PALEONTOLOGY

Order Rodentia Bowdich, 1821
Suborder Myomorpha Brandt, 1855
Family Cricetidae Murray, 1866
Pappocricetodon Tong, 1992

Type Species.—*Pappocricetodon rencunensis* Tong, 1992.

Included Species.—*Pappocricetodon rencunensis* Tong, 1992; *P. schaubi* (Zdansky, 1930); tentatively included, *P. antiquus* Wang and Dawson, 1994.

Emended Diagnosis.—Small cricetids with less enlarged M^1 and M_1 than in other cricetids; upper molar mesoloph well developed, usually extending to mesostyle; anterior lobe of M^1 small, anterocone low, small, and always single cusped, anterior arm of protocone long and generally extending to anterocone, posterior arm of protocone present in many specimens, and anterior arm of hypocone usually ending at buccal side of protocone; M_{1-3} usually with weak ectomesolophid, hypolophid always directed toward hypoconid, and metalophid I of M_{2-3} extending buccally to middle of anterior arm of protoconid; M_1 smallest of lower molars, having only a tiny anteroconid. Incisive foramina short, ending anterior to anterior root of M^1. Masseteric fossa extends forward to a point below M_2 in most specimens.

Pappocricetodon schaubi (Zdansky, 1930)
(Fig. 1, 2)

Holotype.—PIU M3434, right M_2.

Newly Referred Specimens.—14 mandibles (IVPP V11184.1–14) and eight maxillae (IVPP V11185.1–8) (see other referred specimens in Tong, 1992).

Locality and Horizon.—River Section (Locality 1) of Zdansky (1930); 35°04.95′N, 111°50.99′E; Tuqiaogou, east of Zhaili, Yuanqu County, southern Shanxi Province, People's Republic of China; Zhaili Member of the Heti Formation, latest Middle Eocene (ages for the Chinese localities are based on Tong et al., 1995).

Emended Diagnosis.—Slightly larger than *Pappocricetodon rencunensis*; P^4 absent; hystricomorphous skull with large infraorbital foramen; posterior edge of incisive foramen anterior to M^1; anterior lobe of M^1 small but always present, anterocone relatively well developed, posterior arm of protocone usually present and sometimes forming a small closed basin with anterior arm of hypocone; M^2 and M^3 with relatively well-developed parastyle; most specimens of M^3 have a longitudinal crest running forward from hypocone to anterior arm of protocone; M_1 smaller than M_2 and M_3.

Description and Comparisons.—Four fragmentary maxillae preserve parts of the zygoma, infraorbital foramina, and incisive foramina. The posterior edge of the incisive foramen is in a line anterior to the anterior root of M^1. In some eucricetodontines, including *Atavocricetodon atavus* and *Eucricetodon collatus*, the posterior edge of the incisive foramen is more posteriorly situated (Vianey-Liaud, 1974); in *E. asiaticus* the incisive foramen terminates in a line with the anterior edge of the alveolus of M^1 (Lindsay, 1978). The anteroventral surface of the zygoma is large, with a rounded anterior edge and a prominent masseteric tubercle on the anteromedial margin (Fig. 1), which is absent in *Pappocricetodon antiquus* (Wang and Dawson, 1994). The molars do not extend as far anteriorly as the zygomatic plate. This condition is similar to that in *Eucricetodon* and *Pseudocricetodon*, but differs from that in *Eumys elegans*, in which the molars reach anteriorly nearly to the zygomatic plate (Martin, 1980). The ventral edge of the infraorbital foramen is rounded. The shape of the foramen is unlike those of *Eucricetodon* and *Eoeumys*, in which the infraorbital foramen is constricted ventrally, but seems to be closer to those of *Pseudocricetodon* and *Cricetops* (Vianey-Liaud, 1974; Martin, 1980).

The lower jaw is robust (Fig. 2), with the diastema distinctly shorter than the length of the mandibular tooth row. The masseteric fossa extends to below M_2 in most specimens, but in a few reaches to below the posterior edge of M_1. The mental foramen is anterior to M_1, and slightly above the level of intersection of the masseteric lines. The angular process, partially preserved in IVPP V11003.12, is in the same plane as the ramus, the typical sciurognath position.

The dental formula is 1.0.0.3/1.0.0.3. There is no alveolus anterior to M^1 in the known maxillary fragments, differing in this character from *P. antiquus*. The lingual and buccal cusps of the cheek teeth are aligned transversely. This arrangement is unlike that in the European Oligocene cricetids, in which the cusps usually are alternating.

M^1 (Fig. 1) has a smaller anterocone and anterior lobe (prelobe) than in the known late Eocene and Oligocene cricetids of Europe and North America, but both are more distinct than in other described middle Eocene cricetids of China, especially *Pappocricetodon antiquus*. The anterior arm of the protocone (protoloph) is long, reaching to the anterocone. The protoconule on the anterior arm of the protocone is weakly developed or indistinct. The posterior arm of the protocone is present but usually not well developed. In specimens in which it is relatively strong, the posterior arm of the protocone extends either posteriorly to the hypocone or buccally to the anterior arm of the hypocone to form a small closed basin ("protofossette") with the anterior arm of the hypocone or with protoloph I. The posterior arm of the protocone is usually absent in *P. antiquus* (in 132 out of 143 specimens, 92.3%), but present in *P. rencunensis*. The paracone is transversely elongate, and has a weak crest (protoloph I) that extends anterolingually to the anterior arm of the protocone. This also occurs in the other species of *Pappocricetodon*, *P. rencunensis* and *P. antiquus*. The weak crest is also present in *Simimys* of the North American Eocene (the "paralophule" of Lillegraven and Wilson, 1975). The hypocone is ro-
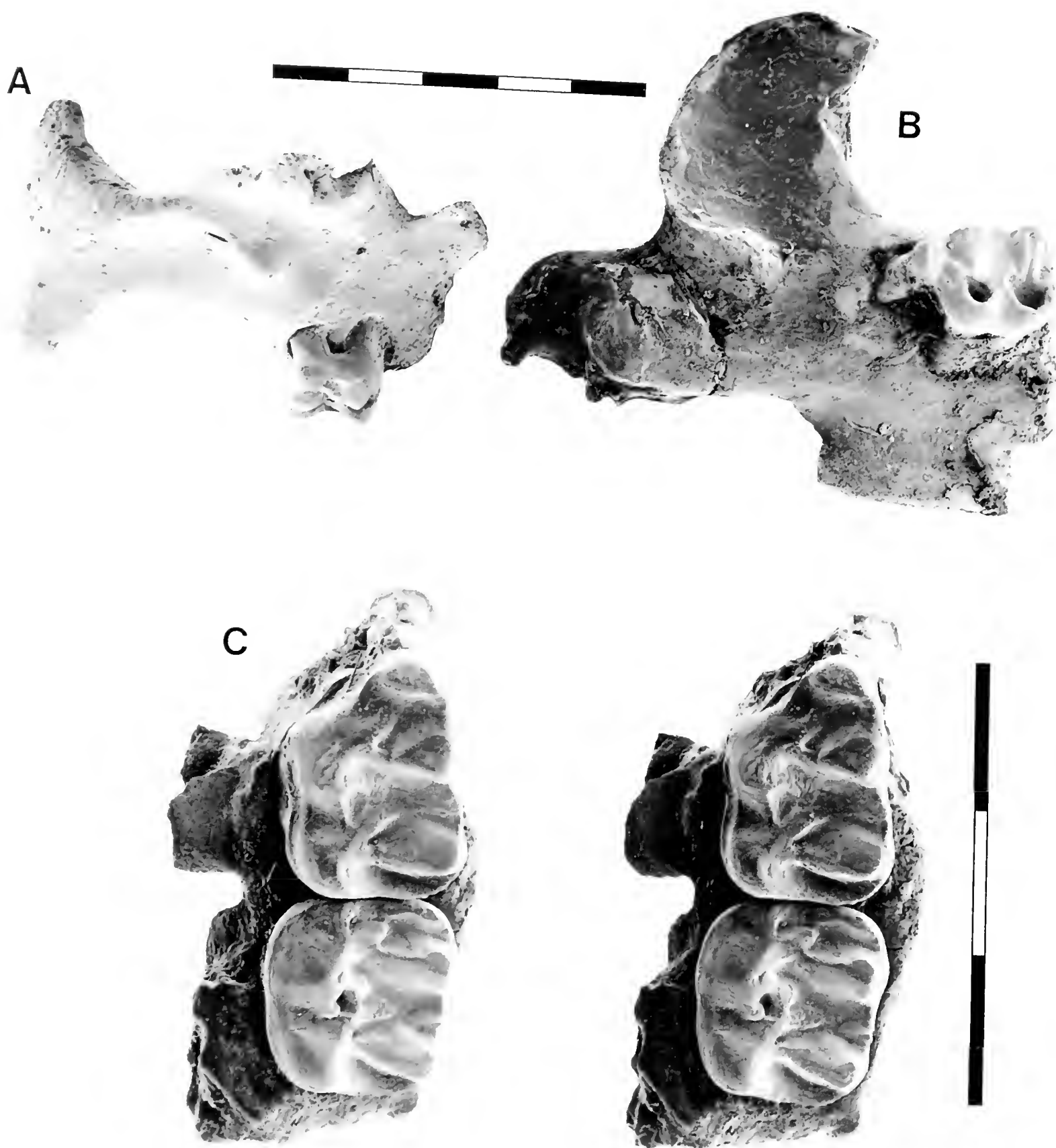
Fig. 1.—*Pappocricetodon schaubi*, maxillae with molar teeth. A. Anterior view of right maxilla, IVPP V11185.7, showing rounded infraorbital foramen. B. Occlusal view of left maxilla, IVPP V11185.4, showing zygomatic root, incisive foramen, and absence of alveolus for P¹. C. Occlusal view of left maxilla, IVPP V11185.3, with M¹⁻² (stereopair). Scale bars in mm; bottom scale bar for C only.

bust. The anterior arm of the hypocone is long, usually ending at the buccal wall of the protocone or occasionally at the anterior arm of the protocone. In *P. rencunensis* this crest does not extend as far anteriorly, but in *P. antiquus* it usually extends far forward, to protoloph I (in 38 out of 143 specimens, 26.6%) or even to the anterior arm of the protocone (in 39 out of 143 specimens, 27.3%) (Wang and Dawson, 1994). The metacone is extended transversely, and the metaloph directed toward the hypocone. The mesostyle is pronounced, but the mesocone is less distinct.

The length and position of the mesoloph vary; usually it is long and closer to the metaloph than to the protoloph.

M² is rectangular, and has a relatively stronger parastyle than in *P. rencunensis* and *P. antiquus*. The "protofossette" occurs more frequently than in the other two species. It may be formed in two different ways: 1) the posterior arm of the protocone may join the anterior arm of the hypocone (IVPP V11003.3), or 2) the forked anterior end of the hypocone arm may join the anterior arm of the protocone and protoloph I (IVPP V8929.19,20). The
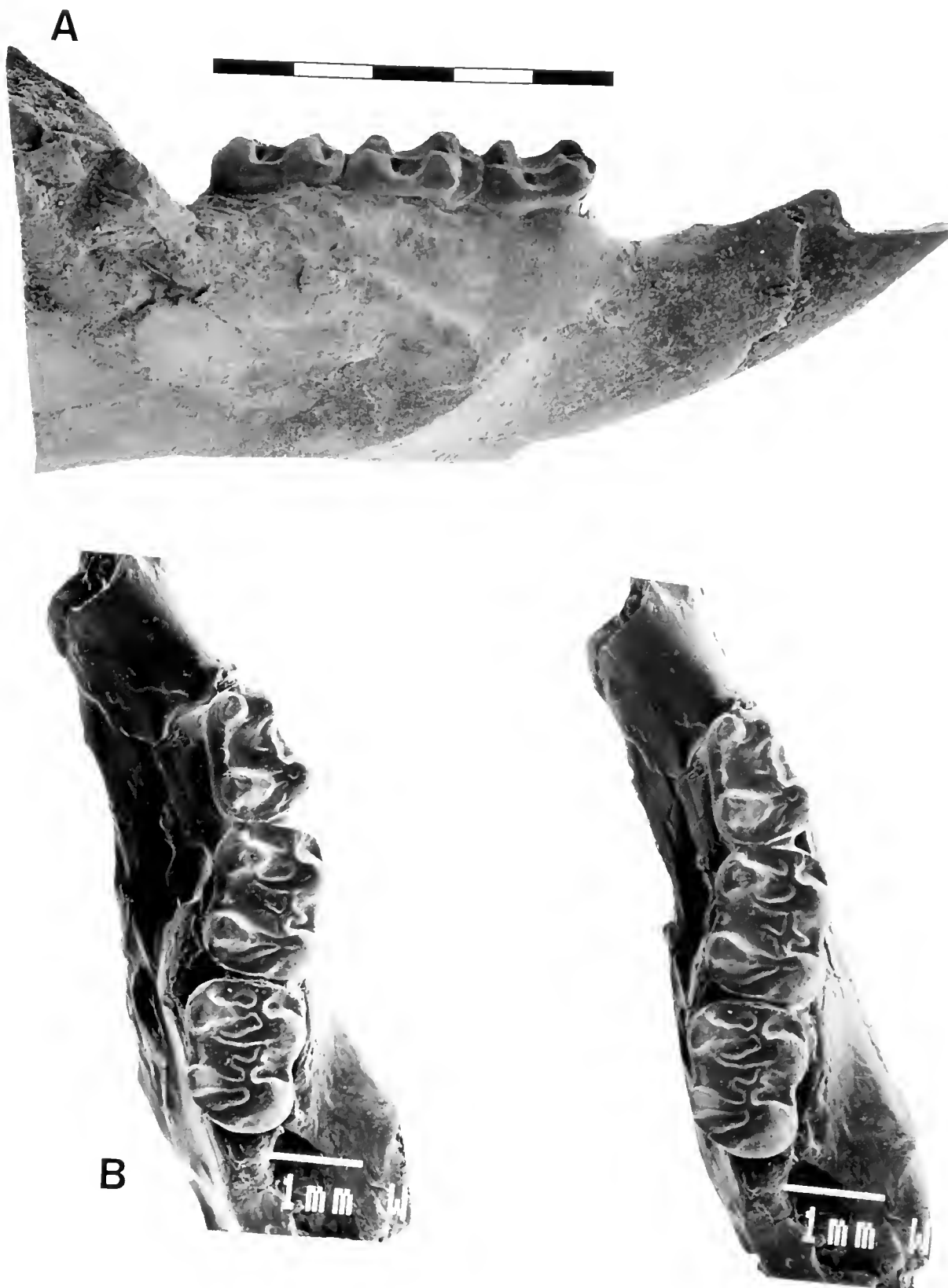
Fig. 2.—*Pappocricetodon schaubi*, mandible with M_{1-3}, IVPP V11184.2. A. Lateral view of right mandible. B. Occlusal view of right mandible with M_{1-3} (stereopair). Scale bar for A = 5 mm.

"protofossette" also occurs on M^2 of some specimens of *P. rencunensis* and *P. antiquus*. Usually the anterior arm of the hypocone ends at the buccal wall of the protocone.

The metacone and hypocone of M^3 are reduced. A longitudinal crest runs from the hypocone to the anterior arm of the protocone, usually forming an elliptical basin with the buccal wall of the protocone.

M_1 is the smallest of the three lower molars (Fig. 2), in contrast to Oligocene cricetids in which it is usually larger than the other lower molars. The trigonid is narrow transversely. The anteroconid is small and low relative to the main cusps, or may even be absent in some specimens. It generally lacks the buccally and lingually descending cingular ridges that characterize M_1 in later cricetids. The small anteroconid does not connect to the proto-

conid or metaconid. Metalophid II (posterior arm of the protoconid) is complete. The hypolophid attaches to either the hypoconid or the ectolophid, as in *Pappocricetodon rencunensis*, whereas in several specimens of *P. antiquus* the buccal end of this crest is posterobuccally curved and meets the posterolophid (in six out of 113 specimens, 5.3%). The mesoconid is distinct, and the ectolophid is complete. Usually the mesolophid is short, and in some specimens a weak ectomesolophid is present.

M_2 is the largest lower molar and has a better developed anteroconid than in *Pappocricetodon rencunensis* and *P. antiquus*. The anteroconid spur is distinct, whereas it is sometimes absent in *P. antiquus*. The anteroconid divides the anterior cingulum into lingual and buccal parts, the former longer than the latter; the lingual part is absent in most early North American cricetids.

The complete protolophid consists of the anterior arm of the protoconid and metalophid I. Metalophid I connects with the anterior arm of the protoconid and sends a spur to the anteroconid near its midpoint. This is the same as in *P. rencunensis* and European Oligocene *Eucricetodon*; in *P. antiquus* metalophid I connects to the anterior arm of the protoconid near the anteroconid, meets the anteroconid directly (IVPP V11018.485), or is not connected with the anterior arm of the protoconid (IVPP

V11018.517). Metalophid I extends to the anteroconid in many eumyines.

M_3 is slightly smaller than M_2, and has a more reduced talonid. The ratio of length of M_3 to length of M_2 is close to that of the North American *Eumys* and the European *Pseudocricetodon*, but greater than in *Atavocricetodon* and European species of *Eucricetodon* (Tong, 1992).

DISCUSSION

Cricetids have been widely distributed in the Holarctic since the beginning of the Oligocene. In Europe the earliest cricetid, *Atavocricetodon atavus*, first appears in the earliest Oligocene, mammalian reference level MP 21, just after the Grande Coupure (Priabonian–Rupelian or approximately the Chadronian–Orellan boundary; see Brunet and Vianey–Liaud, 1987; Woodburne and Swisher, 1995; Freudenthal, 1996). In North America the first appearance of undoubted cricetids was in the late Eocene Chadronian North American Land Mammal Age (NALMA) (Martin, 1980; Storer, 1994; two teeth of late middle Eocene age, Duchesnean NALMA, referred to *Eumys* by Storer, 1988, have been transferred to the Sciuravidae by Dawson, in press). In Asia, where the oldest known cricetids occur, recent discoveries and study of Eocene cricetids have increased our knowledge of the early evolution of the family. Two species from the late Eocene (Ulangochuian) of Yunnan Province were reported by Wang and Meng (1986). New records were added from the Yuanqu Basin of Shanxi Province (Tong, 1992) and from middle Eocene fissure deposits of Jiangsu Province (Wang and Dawson, 1994). Cricetid history in Asia can now be traced back even farther, to early Irdinmanhan age (Tong, 1997).

THE ASIAN RECORD

Reexamination of *Pappocricetodon*, the oldest currently described cricetid genus, shows that development of the family was well underway in Asia during the middle Eocene. Comparisons between the three species now referred to *Pappocricetodon* reveal that *P. antiquus* from Jiangsu Province is distinctly different from the two species from the Yuanqu Basin, *P. rencunensis* and *P. schaubi*. Wang and Dawson (1994) specified differences of the Jiangsu specimens from the Yuanqu species as follows: *P. antiquus* is smaller; presence of P4 is indicated by an alveolus in all known maxillae; upper molars have a bulbous protocone and a less well-developed mesoloph; M1 is less enlarged and has a

smaller anterior lobe and anterocone; M1–2 have a long mure and a long, oblique lingual valley; M3 is less reduced and has a more distinct metacone, an indistinct, less buccally shifted hypocone, and a shallower lingual valley; lower molars lack an ectomesolophid and have a rather transverse hypolophid that connects to either the hypoconid or the posterolophid; M1 is less enlarged and has a less distinct anteroconid; M3 is less reduced. Whereas *P. antiquus* shows several traits in which it is more primitive than the Yuanqu Basin species, it also has some characters that can be interpreted as derived. For example, M1 of the Sharamurunian species, *P. rencunensis*, has a shorter anterior arm of the hypocone (mure) which ends at the posterobuccal corner of the protocone in many specimens. This arm is longer in the later species, *P. schaubi*, and usually extends to the buccal side of the protocone. In *P. antiquus* the anterior arm of the hypocone is variable, and may extend to the protoloph, to the lingual crest of the paracone, or to the buccal side of the protocone. This elongated crest in *P. antiquus* results in a deep lingual valley (sinus) entering the crown obliquely. The lingual valley of the upper molars is relatively deep in nearly all Oligocene cricetids, so the deep lingual valley and long anterior arm of the hypocone are thought to be derived characters relative to the Yuanqu species. Absence of the posterior protocone arm in *P. antiquus* may also be a derived character, for it is present in still older cricetids from the early Irdinmanhan (Tong, 1997). Metalophid I on M_2 of *P. antiquus* extends anterobuccally to the anteroconid in many specimens, a morphology that also occurs in North American Paleogene cricetids assigned to the subfamily Eumyinae by Martin (1980). In both species from the Yuanqu Basin, metalophid I usually extends buccally to meet the anterior arm of the protoconid. The last molars in *P. antiquus* are less reduced than in the Yuanqu species.

These differences from *Pappocricetodon rencunensis* and *P. schaubi* led Wang and Dawson (1994)

to suggest that *P. antiquus* appears to be a sister group to the two others. Perhaps it should be differentiated as a separate genus. At present, *P. antiquus* and *P. schaubi* are known by relatively complete material, including maxillae and mandibles, but only isolated teeth are known for *P. rencunensis*. Until this species is more completely represented so that shared characters, such as presence or absence of P^4, can be more thoroughly investigated, all three species are here retained in *Pappocricetodon*.

THE EUROPEAN AND NORTH AMERICAN RECORDS

Pappocricetodon schaubi differs from the Oligocene cricetids of Eurasia and North America in a number of features including the following primitive characters: brachydont cheek teeth, less enlarged M^1, M$_1$ smaller than other lower molars, anterior lobe of M^1 smaller and anterocone lower and less well developed, protoloph I usually joined to anterior arm of protocone, anterior arm of hypocone long, sinus of upper molars shallow, anteroconid of M$_1$ tiny, anterior spur of hypoconulid absent.

Ünay-Bayraktar (1989) proposed a classification of European Paleogene Muroidea in which she allocated the early cricetids into the four families—Melissiodontidae, Pseudocricetodontidae, Eucricetodontidae, and Heterocricetodontidae. A contrasting arrangement of European Oligocene muroids was proposed by Freudenthal et al. (1992), with the family Cricetidae divided into three subfamilies—Paracricetodontinae, Eucricetodontinae, and Pseudocricetodontinae. A distinct family Melissiodontidae was also recognized, and the genus *Adelomyarion* was considered to be of uncertain familial reference. Martin (1980) discussed the Oligocene and early Miocene radiation of cricetids in North America, and proposed a classification for them. Although a phylogenetic analysis of these varied European and North American early muroids is not the focus of this paper, the relationships of early cricetids of Asia with those of Europe and North America are briefly considered below.

The early cricetids of Europe are closer to the Yuanqu cricetids, *Pappocricetodon rencunensis* and *P. schaubi*, than they are to the North American species in having: less bulbous main cusps; a more transverse, more distinctly developed protoloph; reduced metacone of M^3; and a transversely elongated metalophid I of M$_{2-3}$. The European cricetids are, however, derived relative to *Pappocricetodon*. *Atavocricetodon atavus* is the oldest cricetid in the European record, first appearing in MP 21. Specimens of this species from the Tongrian of Hoogbutsel (Freudenthal, 1988) show that M^1 and M$_1$ are enlarged relative to these teeth in the Yuanqu species (ratio of length M^1/M^2 is 133.9, as opposed to 112.2 in *P. rencunensis*, 117.8 in *P. schaubi*; ratio of length M$_1$/M$_2$, 113.4, as opposed to 95.3 in *P. rencunensis*, 97.7 in *P. schaubi*); the mure is closer to the midline of the tooth; M$_3$ is distinctly reduced (ratio of length M$_3$/M$_2$, 92.6, as opposed to 98.8 in *P. rencunensis*, 95 in *P. schaubi*).

The European Oligocene cricetid *Pseudocricetodon* first appears in mammalian reference level MP 23 (Brunet and Vianey-Liaud, 1987). In this genus the cheek teeth are relatively lophodont. Compared to the Yuanqu species it has a well-developed anterocone and large anterior lobe on M^1, the anterior cingulum is quite reduced lingually on M$^{2-3}$, and a rather enlarged anteroconid is present on M$_1$. These characters of early eucricetodontines and pseudocricetodontines can be regarded as derived. There is a considerable gap in both morphology and time of appearance between *Pappocricetodon* on the one hand and *Atavocricetodon*, *Eucricetodon*, and *Pseudocricetodon* on the other, but there is nothing known to suggest that the Asian middle Eocene cricetids are not related to these genera, which appeared in Europe after the Grande Coupure. The late Eocene cricetids from Yunnan, *E.? meridionalis* and *E.? leptaleos*, probably are intermediate in morphology, having many primitive characters relative to the known European species (Wang and Dawson, 1994), but showing some advanced characters compared with *Pappocricetodon rencunensis* and *P. schaubi*.

Two North American genera of cricetids have relatively well-documented appearances in the Chadronian (late Eocene). Both *Scottimus* and *Eumys* (Korth, 1981; Storer, 1994) have been recognized, although this generic separation may overstate the morphological differences between Chadronian members of the family. Nonetheless, at this time North American cricetids were somewhat diversified and quite specialized. M^1 is relatively more enlarged than in the approximately contemporaneous Asian species *Eucricetodon? meridionalis* and *E.? leptaleos* from the early Ulangochuian of Yunnan, and the sinus of M^3 folds deeply between the protocone and hypocone. The anterior and posterior walls of the main cusps are rather steep. The buccal part of the anterior cingulum is emphasized on M$^{2-3}$ of *Eumys* and *Eoeumys*, and the lingual part is missing. In *Scottimus*, as in *Pappocricetodon* and *Eucricetodon*, the relatively weaker anterior cingulum

is complete, extends to both the buccal and lingual margins of the tooth, and is divided into buccal and lingual parts by the anterocone. Longitudinal lophs are present in the upper molars of *Scottimus*, and "transverse lophs on lower molars tend to be oriented more anteroposteriorly" (Korth, 1981), while in *Eumys* and *Eoeumys* the longitudinal loph of the upper molars is lacking and the transverse lophs are buccolingually elongated. The late Eocene cricetids of North America retained some primitive characters, such as the protoloph joining the anterior arm of the protocone (anterior connection) on M^{2-3} of *Scottimus*, and a more distinct metacone of M^3 than in *Pappocricetodon*. The latter character could also be regarded as secondarily enlarged, because a comparably well-developed metacone is not present on

M^3 in *Pappocricetodon* and other early cricetids. If this is the case, the cricetids that appeared in North America during the Chadronian could have originated from the currently known middle Eocene cricetids of Asia.

The North American late Eocene species are closest in some characters to *Pappocricetodon antiquus* of the known Asian Eocene taxa. *Pappocricetodon antiquus* has more bulbous main cusps than other Asian species, a deeper sinus on the upper molars, a slightly more distinct metacone of M^3, and metalophid I on M_{2-3} usually extending to the anteroconid. The species of *Pappocricetodon* illustrate the possibility that the North American cricetids also can be traced to Asia and add evidence for faunal interchange between Asia and North America during the Chadronian.

ACKNOWLEDGMENTS

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HYPSAMASIA SENI (MAMMALIA: EMBRITHOPODA) AND OTHER MAMMALS FROM THE EOCENE KARTAL FORMATION OF TURKEY

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ABSTRACT

The newly discovered vertebrate fauna from the Eocene-age Kartal Formation of central Turkey promises to fill a critical gap in our knowledge of Old World mammalian biogeography. The fauna includes fish, crocodiles, snakes, lizards, and mammals. Among the ten taxa of mammals recovered to date are a marsupial, three species of ungulates (of uncertain ordinal affinities), a proboscidean, two species of embrithopod, and three new species that probably represent two additional orders. A new genus and species of embrithopod is described here. The new genus, represented by associated upper premolars and molars, is closest to *Palaeoamasia*, one of two mammals previously known from the Paleogene of Turkey, and is included in the family Palaeoamasiidae. This adds to a growing body of evidence that suggests that the Embrithopoda, best known from Africa and long considered endemic to that continent, had a more cosmopolitan evolutionary history. The Eocene mammals known thus far from Turkey show affinities with both European and African groups, but as yet there is no evidence of contact with mammalian faunas from eastern Asia or Indo-Pakistan.

INTRODUCTION

Paleobiogeography is a key element of Paleogene mammalian evolution. Not only is it critical to our understanding of the origin of major groups, but it is of major importance in reconstructing their later evolutionary history. In many instances, however, our understanding of mammalian distributions and dispersal histories is hindered by a geographically and temporally incomplete fossil record. A case in point is the Eocene history of circum-Tethyan faunal interchange among Asia, Africa, and Europe.

Faunal exchange among Asia, Africa, and Europe is thought to account for the cosmopolitan distribution of archaic forms, such as palaeoryctid "insectivores" and adapisoriculids (?late Cretaceous–Paleocene dispersal) as well as for the first occurrences of a number of modern orders of mammals, including artiodactyls, perissodactyls, and primates (late Paleocene–earliest Eocene dispersal) (e.g., Pilgrim, 1941; Szalay and McKenna, 1971; Gingerich, 1986, 1989; Gheerbrant, 1988, 1990, 1991a, 1991b, 1992; Gheerbrant and Russell, 1989, 1991; Krause and Maas, 1990; Sigé et al., 1990). Later, during the middle and late Eocene, faunal provinciality increased, probably as a result of climatic change and the formation of geographic barriers, although some more limited faunal exchange may still have occurred (e.g., Savage and Russell, 1983; Legendre, 1989; Hooker, 1992; Stucky, 1992). By the end of the Eocene, tectonic and climatic factors apparently facilitated increased faunal exchange between European faunal provinces and between Asia and Europe (e.g., Heissig, 1979; Hooker, 1987, 1992).

Although this broad outline of early Tertiary circum-Tethyan biogeography is generally accepted, the details are much less clear, in part because of critical temporal and geographic gaps in the fossil record of many early Tertiary groups (e.g., Gheerbrant, 1987, 1990; Gheerbrant and Russell, 1989; Holroyd and Maas, 1994). Thus, important questions remain concerning the origin and dispersal histories of the earliest artiodactyls, perissodactyls, and primates, the paleobiogeographical history of groups such as African hystricomorph rodents, hyaenodontid creodonts, anthracotheriid artiodac-

tyls, anthropoid primates, and didelphid marsupials, and the origins and early biogeographic histories of groups traditionally considered endemic to Africa, including prosboscideans and embrithopods.

Paleogeographic reconstructions of the early Tertiary circum-Tethyan region (e.g., Dercourt et al., 1986; Smith et al., 1994, Ricou, 1995) indicate significant marine barriers to intercontinental dispersal by terrestrial mammals. Consequently, most discussions of early Tertiary trans-Tethyan dispersal of terrestrial mammals invoke "sweepstakes" dispersal, by way of hypothesized island arcs (e.g., Simons and Bown, 1984; Gingerich, 1986; Gheerbrant, 1990; Crochet et al., 1992; Thewissen and McKenna, 1992; Holroyd and Maas, 1994). Unfortunately, the paleogeographic data are insufficient to allow such scenarios to pinpoint the timing of, the specific routes available for, or the direction of mammalian dispersal. These missing data can only be provided by discovery of faunas of appropriate ages in key regions.

One such key region is Central Anatolia, located in the north-central region of modern-day Turkey (Fig. 1). Until recently, only a few, isolated mammalian fossils had been recovered from its early Tertiary continental deposits. A newly reported ver-
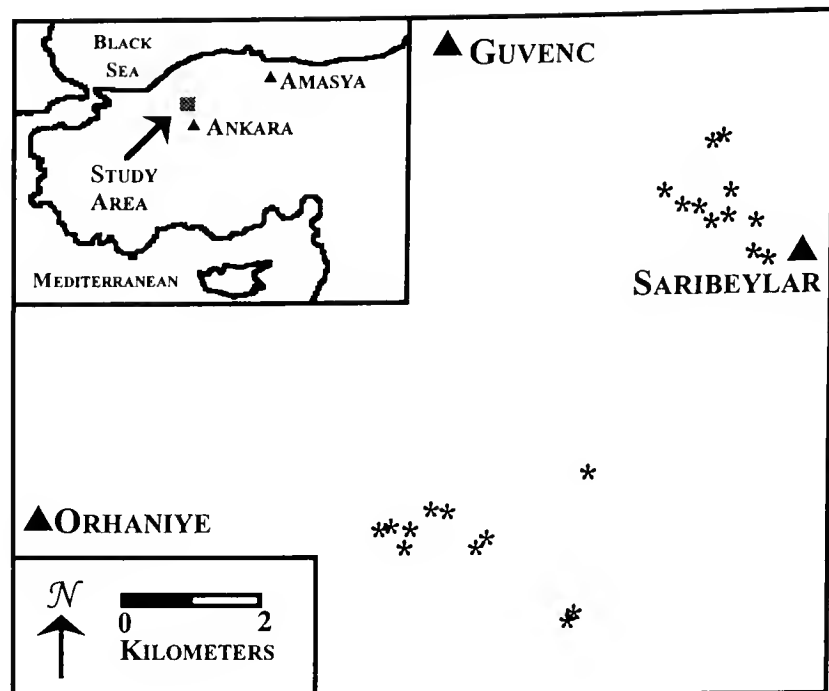
Fig. 1.—Location of major fossil vertebrate localities (asterisks) in the Kartal Formation, Ankara, Turkey. Inset map shows location of study area.

tebrate fauna from the Kartal Formation in Central Anatolia (Kappelman et al., 1996) promises to fill some of the critical gaps in our knowledge of Eocene circum-Tethyan mammalian evolution and biogeography.

PALEOGENE VERTEBRATE FOSSILS IN TURKEY

Prior to the discovery of the Kartal Formation vertebrate fauna, the only Paleogene vertebrates reported from Turkey were three species of large mammals, all recovered from middle Eocene (?Lutetian) lignite deposits near the town of Amasya (see Fig. 1). These include two embrithopods, *Palaeoamasia* spp., known from a total of ten specimens (Sen and Heintz, 1979; Radulesco and Sudre, 1985), and a haplobunodontid artiodactyl, *Parabunodon*, known from a single specimen (Ducrocq and Sen, 1991). Although no other vertebrate specimens have been recovered from these localities, these fossils nevertheless are of considerable paleobiogeographic interest. For example, the occurrence of *Parabunodon*, which represents the easternmost occurrence of the European family Haplobundontidae, is relevant to our understanding of the early Tertiary dispersal of artiodactyls between Europe and Asia (e.g., Thewissen et al., 1987). Likewise, discovery of the embrithopod *Palaeoamasia* raises intriguing questions concerning the origin and relationships of arsinoitheres, long considered endemic to Africa. Furthermore, the occurrence of embrithopods in the

middle Eocene of Turkey and in the late Eocene of Romania (Radulesco et al., 1976; McKenna and Manning, 1977; Radulesco and Sudre, 1985) lends some support to the idea of a southeastern European faunal province, independent of western Europe during this time (Radulesco and Sudre, 1985; Heissig, 1990).

In 1994, vertebrate fossils were discovered in the Paleogene Kartal Formation in the state of Ankara, Turkey. The Kartal Formation consists largely of continental clastics, and is located stratigraphically between the underlying Late Cretaceous marine Tesrekyayla Formation and the overlying Uzunçarsi Formation and marine Akpinar Formation; the latter is described as middle Eocene in age (Koçyigit, 1991). The initial discovery and subsequent field work in 1995 have yielded the most diverse Eocene vertebrate fauna known from either Turkey or its immediate neighbors (Kappelman et al., 1996). The vertebrate fauna from the Kartal Formation, in addition to scarce remains of fish, includes more abundant remains of turtle, lizards, snakes, crocodiles, and at least ten species of mammals (Table 1).

Osteichthyes
Chelonia
Lacertilia
Serpentes
Crocodylia
Marsupialia
  Didelphidae
    Herpetotheriinae n. gen. and sp.
?Marsupialia indet.
Ungulata indet., three species
Proboscidea indet.
Embrithopoda
  Palaeoamasiidae
    Hypsamasia seni n. gen. and sp.
  ?Palaeoamasiidae gen. and sp. indet.
Mammalia, incertae sedis, two species

Among the mammalian species is a new herpetotheriine marsupial, represented by isolated upper and lower molars (Kappelman et al., 1996), and three species of ungulate of uncertain ordinal affinities, which are currently under study. These ungulates are represented by upper and lower jaws and a skull fragment. The remaining mammalian taxa recovered from the 1994 and 1995 field seasons are not, with the exception of the new species of embrithopod described below, known from material adequate to warrant their formal naming at this time. However, the unique nature of some of these specimens, and the importance of this fauna in the biogeographic history of Paleogene Old World mammals, warrant their description here.

All vertebrate specimens recovered from the Kartal Formation are housed in collections of the Museum of Anatolian Civilizations (Anadolu Medeniyetleri Müzesi), Ankara, Turkey.

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758
Order Embrithopoda Andrews, 1906
Family Palaeoamasiidae Sen and Heintz, 1979
Hypsamasia, **new genus**

Type and Only Species.—*Hypsamasia seni*, n. sp.
Age and Distribution.—Middle(?) Eocene, Kartal Formation, Turkey.

Etymology.—Greek *hypsos* (height), in reference to the high-crowned cheek teeth; and Latin *Amasia*, Roman name for the Turkish town and province of Amasya; in reference to *Palaeoamasia* and the familial affinities of the genus.

Diagnosis.—Palaeoamasiid with high-crowned teeth. Protocone and hypocone are distinct and large, not fused into para- and metaloph.

Discussion.—Sen and Heintz (1979) and Court (1992) discussed the unique embrithopod dental morphology: it includes nonmolariform upper premolars combined with strongly bilophodont upper molars in which the lophs consist mainly of connections between paracone and parastyle, and between metacone and mesostyle. This morphology is shared by all genera for which upper dentitions are known (*Arsinoitherium* and *Palaeoamasia*). *Hypsamasia* is also characterized by these traits. In addition, it shares with *Palaeoamasia* the presence of a large molar protocone and hypocone. *Hypsamasia* is larger than either species of *Palaeoamasia* (see Radulesco and Sudre, 1985) and its molars are higher crowned. *Hypsamasia* cannot be compared directly with the late Eocene Romanian *Crivadiatherium* (see Radulesco et al., 1976), for which only lower teeth are known, but the latter genus has low-crowned teeth, whereas those of *Hypsamasia* are high crowned. In light of the newly discovered diversity of Turkish embrithopods, we concur with the conclusion of Kaya (1995) and consider the subfamily Palaeoamasiinae Sen and Heintz, 1979 distinctive at the familial level. *Palaeoamasia*, *Crivadiatherium*, and *Hypsamasia* thus constitute a family of embrithopods distinct from the African Arsinoitheriidae.

Hypsamasia seni, **new species**
(Fig. 2, 3)

Holotype.—AK 95-52; right side: P^{2-3}, fragments of P^4–M^1; left side: central portion of M^1, anterior half of M^2, and fragments of unerupted M^3. Individual teeth and fragments were found associated, but not in anatomical contact due to severe erosional damage. Only those fragments that had clear matching contacts were glued, and some of the remaining fragments are not described here. The type and only specimen of this new species was discovered in 1995.

Type Locality and Horizon.—Locality AK-33, 6 km southwest of the village of Saribeylar, middle(?) Eocene, Kartal Formation, Ankara, Turkey.

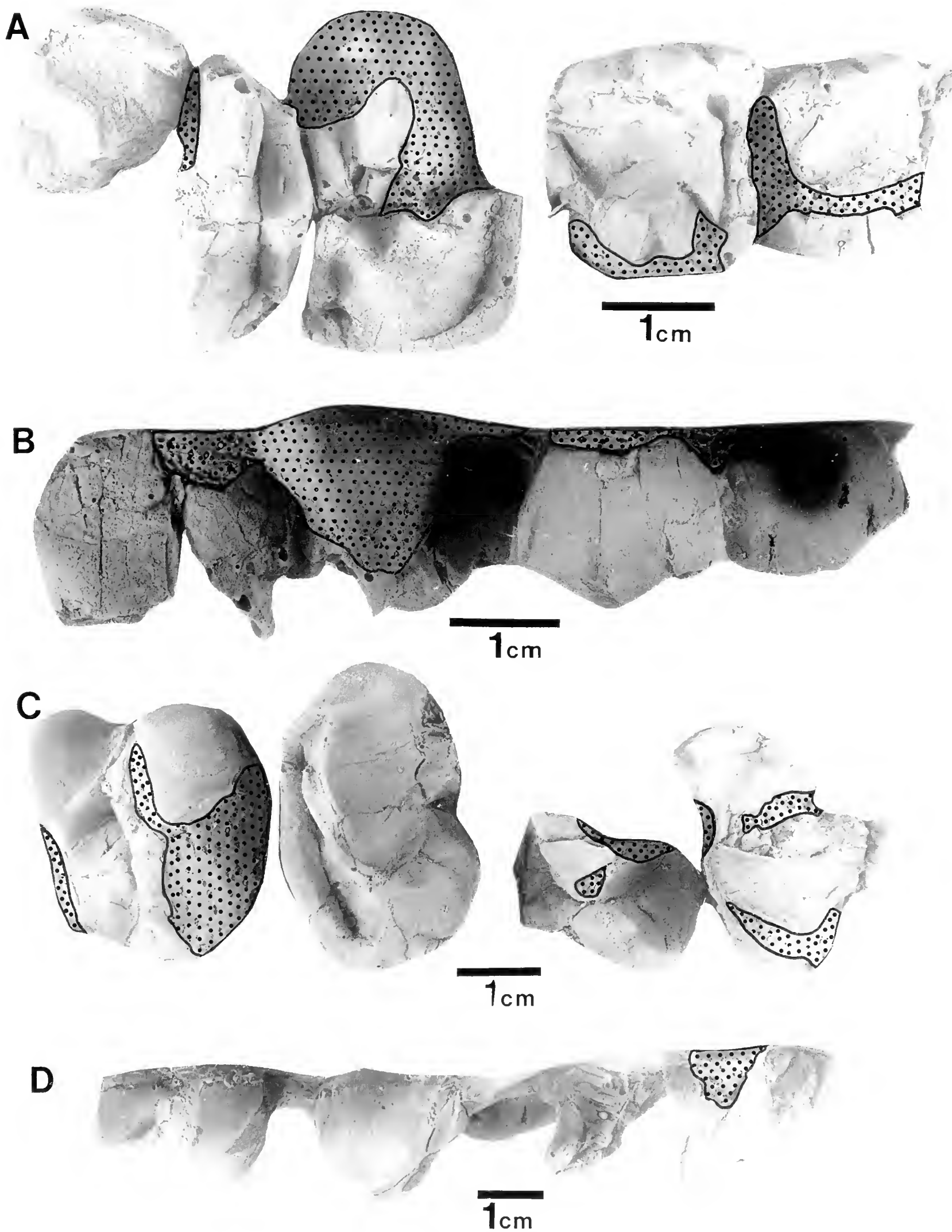*Etymology.*—Specific name is in reference to Dr. Sevket Sen,

Fig. 2.—*Hypsamasia seni*, n. gen. and sp., AK 95-52, holotype. Stippling indicates reconstructed areas. A. Right P^2–M^1, occlusal view. B. Right P^2–M^1, buccal view. C. Left M^1–M^3, occlusal view. D. Left M^1–M^3, buccal view.

in recognition of his important contributions to the vertebrate paleontology and geology of western Asia.

Diagnosis.—*Hypsamasia* is monospecific and we do not differentiate between generic and specific diagnosis.

Description.—P[2] has a crescentic protocone that is connected to the paracone by the preprotocrista. A paraconule may have been present, but this area of the tooth is damaged. The postprotocrista extends posterior from the protocone and probably reached the posterior side of the tooth; it is not directed toward the metacone. Paracone and metacone are similar in size, and conical in morphology. They are connected by a crest that extends anteriorly to a large and well-worn parastyle. The anterior cingulum was probably complete; it descends lingual from the parastyle, ending just buccal to the protocone. There is no lingual or buccal cingulum. The buccal crown height is greater than the lingual crown height. The lingual wall of the protocone was disconnected from the rest of the tooth by erosion and displaced a few millimeters lingually. Therefore, the width of the tooth cannot be measured. The posterior side of the tooth is missing and thus no length can be determined.

P[3] is similar to P[2] in the arrangement of the paracone, metacone, and protocone, and is less damaged. Posteriorly, the postprotocrista reaches the posterior cingulum, and there is no metaconule. The anterior cingulum is strong and complete, and there is a large paraconule on the preprotocrista. This crest is much stronger than the postprotocrista. The tooth is damaged lingually, but its length can be determined: 20.4 mm.

Only the lingual side of P[4] is preserved. It has a large protocone and a strong preprotocrista that reaches the paraconule. The anterior cingulum is also strong. The postprotocrista extends to the metaconule and there is a cingulum lingual to this cusp, but not posterior to it. Another tooth fragment probably represents part of the posterior side of P[4]. There is no direct contact with the lingual fragment, but the interstitial wear facet matches that of the anterior side of the inferred right M[1]. This P[4] fragment includes the posterior side of the metacone and a fragment of the large posterior cingulum. As in the anterior premolars, the metacone is higher than the protocone.

An anterior fragment of the right M[1] was identified on the basis of its morphological similarity but smaller size and more extensive wear when compared to the left M[2]. This fragment has a strong cingulum anterior to the protocone. The protocone is high and a loph extends buccal to it, presumably from the paracone to the parastyle (cusp homologies as discussed by Court, 1992). The paracone is not preserved. The cingulum joins the protoloph buccally. A second tooth fragment may represent the buccal side of the anterior loph of M[1]. It shows an anteriorly convex, strongly worn loph. A dentine fragment projecting from the concave side of this specimen indicates that it does not represent the posterior loph of an upper molar, although it may represent a lower molar.

The central part of the left M[1] is also preserved. It shows the entire posterior wall of the anterior loph. This structure is posteriorly concave. The protocone appears worn lingually, exposing a large area of dentine. The anterior loph is anteriorly inclined. Its posterior aspect bears a strong centrocrista that extends down to the mesostyle. Lingually, the posterior loph ends immediately buccal to the hypocone. This cusp is so close to the loph that with increasing wear the two would fuse. Approximate width of M[1] is 33.9 mm. Another fragment probably represents the buccal

side of the posterior loph of the left M[1]. It shows that the mesostyle forms a ridge reaching down to the base of the tooth and that a similar ridge is present at the position of the metacone.

The anterior half of the left M[2] is preserved intact. It shows an anteriorly convex loph that is somewhat worn and extends between parastyle and paracone. Immediately lingual to the paracone is the protocone, which has steep sides. An enamel crest descends the protocone to the anterior cingulum. This cingulum is strong, and reaches buccally to the parastyle. There is no lingual cingulum, and the tooth is much higher buccally than lingually. The anterior loph slopes posteriorly. The posterior side of the loph has two strong crests that descend to the central basin of the tooth posteriorly. The more buccal of these ends in the parastyle, whereas the lingual represents the centrocrista. The trigonid basin is deep as a result of the height of the lophs. Width of this tooth is 41.5 mm.

Preserved fragments of M[3] are completely unworn, light gray in color (the associated molars and premolars show wear and are dark grey or black in color); thus, the M[3] was apparently not erupted. An anterolingual fragment shows the lingual side of the anterior loph, and well below it the protocone, which has an anteroposteriorly elongated summit. The concavity of the anterior side of the tooth suggests that the basin posterior to the anterior cingulum was wider than in M[2]. Two lingual fragments of the posterior loph of M[3] were found in close contact. They show that the posterior loph was convex anteriorly, and that its summit sloped down gently lingually, unlike the anterior loph which ends abruptly. The area for the hypocone is not preserved, but a small segment of the posterior cingulum is present. Another fragment probably represents the buccal side of the posterior loph of M[3], based on the microscopic similarity of the cross section of the enamel of its lingual extreme to that of the buccal extreme of the other fragment. The buccal fragment shows a sharp crest posteriorly that extends to the posterior side of the tooth (mesostyle), and anterobuccal to this a low cusp that was probably on the cingulum. This cusp does not occur in any other embrithopod, and may represent a unique feature. However, we do not include it in the diagnosis, because it is possible that this fragment was misidentified.

Scanning electron microscopy of a lightly etched enamel fragment demonstrated that *Hypsamasia* molars are characterized by modified radial enamel (MRE) (Fig. 3). MRE consists of prisms that are parallel to one another and separated by thick sheets of interprismatic enamel, with interprismatic crystallites oriented nearly perpendicular to crystallites within prisms. MRE also is found in the African embrithopod *Arsinoitherium* (Pfretzschner, 1992).

Discussion.—*Hypsamasia seni* differs from *Palaeoamasia kansui* mainly in its larger size and higher-crowned teeth. This is especially noticeable in the molar protocone, which has gently sloping walls in *Palaeoamasia*, but is high and has steep walls in *Hypsamasia seni*.

Hypsamasia seni is not the only embrithopod of the Kartal Formation. A second species is documented by a fragmentary lower molar (AK 94-2) and a lower premolar (AK 94-5) found at Locality AK-1. Like *Hypsamasia*, the enamel of this species consists of the modified radial enamel type. The unnamed species is smaller than any other known em-
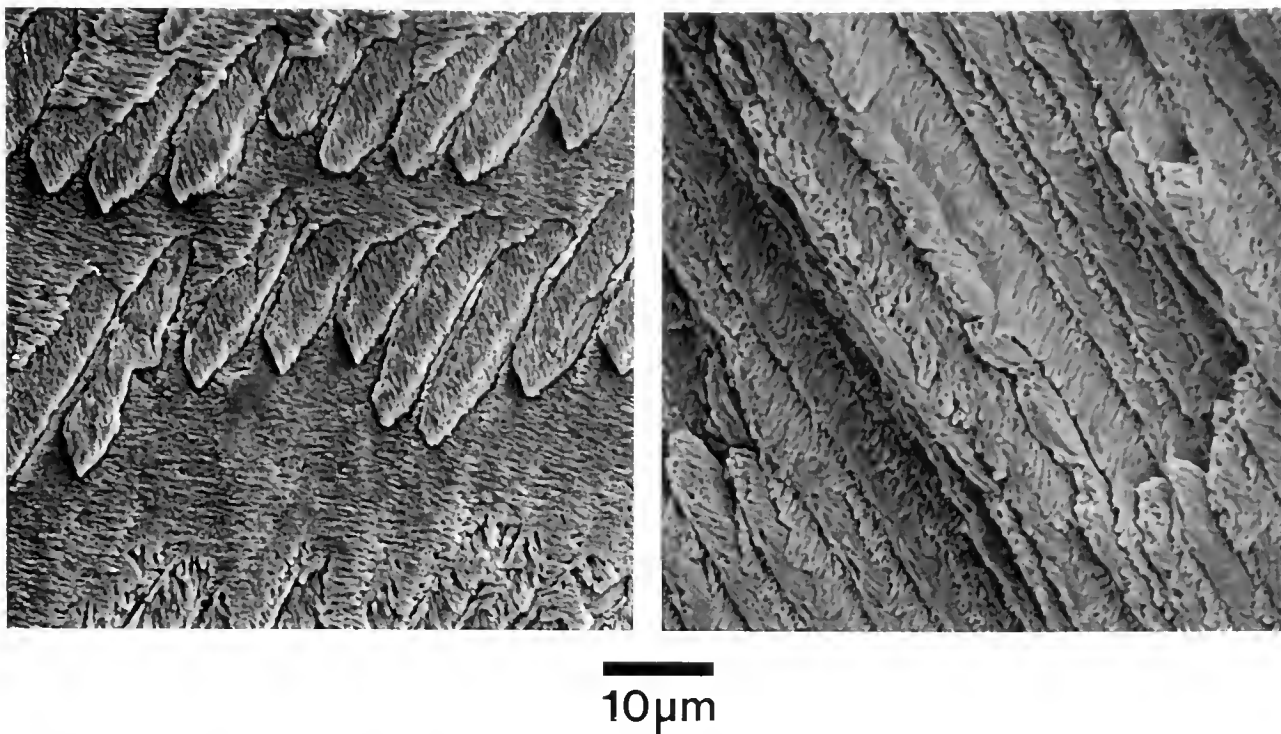
10μm

Fig. 3.—*Hypsamasia seni*, n. gen. and sp. Scanning electron micrographs of longitudinal section of molar enamel illustrating modified radial enamel.

brithopod (lower molar width 12.8 mm), but these remains are inadequate for a detailed comparison.

Embrithopods are of considerable biogeographical importance. Although best known from North Africa (Tanner, 1978), they range from Romania (Radulesco et al., 1976; Radulesco and Sudre, 1985) into central Africa (Pickford, 1986) and the Arabian Peninsula (Thomas et al., 1989). However, most or all of these are younger than the Turkish embrithopods (Sen and Heintz, 1979, this paper), and the Turkish palaeoamasiids are probably more primitive (Court, 1992).

McKenna and Manning (1977) referred *Phenacolophus* from Mongolia to Embrithopoda, but this was questioned by Radulesco and Sudre (1985). Although certain similarities exist, we agree with Radulesco and Sudre (1985) that the relation of phenacolophids to embrithopods remains to be substantiated.

Order Proboscidea
Genus and species indeterminate
(Fig. 4)

Material.—AK 95-1, probable right dI₁, from Locality AK-1, Kartal Formation, Ankara, Turkey.

Description.—This right lower incisor (most probably a deciduous first incisor, following homologies of Tassy, 1987) is single cusped and tapers from a narrow tip to a broader, oval base. The specimen is broken at the base, just below the ventral enamel–dentine junction; the maximum width at the base is 9.4 mm. That it is strongly procumbent is suggested by the very oblique orientation of the enamel–dentine junction relative to the tooth axis. The enamel–dentine junction is asymmetric: enamel

covers the entire lateral face of the tooth but is restricted to the upper third of the medial surface and tapers down to the base of the tooth at the ventrolateral edge. On the medial surface a strong crest runs from the tip of the tooth posteriorly to the enamel–dentine junction. The lateral surface is smooth and slightly convex, with distinct perikymata (surface manifestations of incremental growth lines) visible on its unworn enamel surface. A sharp crest on the dorsal surface of the lateral edge of the tooth extends from the tip to the cervix and bears five blunt denticulations. Each of the cervical three denticulations are twinned.

Discussion.—Except for its much smaller size, this isolated incisor is strikingly similar to that of the late Eocene *Palaeomastodon* (*Phiomia*) *serridens* (see Andrews, 1906:pl. XVIII, fig. 4). It also is similar to, but smaller than, a single lower incisor with an outer convex, crenulated border reported from the early Oligocene Thaytiniti locality in Oman and attributed to Proboscidea indet. (Thomas et al., 1989). A denticulated lateral edge is also characteristic of some other proboscideans, including some gomphotheres and ambelodontids (Tassy, 1987). Based on these similarities, we attribute the Kartal specimen to Proboscidea, indet.

Supercohort ?Marsupialia
Genus and species indeterminate
(Fig. 5A)

Material.—AK 95-19, left M¹ or M², Locality AK-21, Kartal Formation, Ankara, Turkey.

Description.—AK 95-19 is a small (length 3.2 mm, width 3.9 mm), bunodont tooth with three major cusps (protocone, paracone, and metacone) and a metaconule. Five distinct stylar cusps are found on the broad stylar shelf and are designated A through E from anterior to posterior. Their relative sizes are: D > B ≫
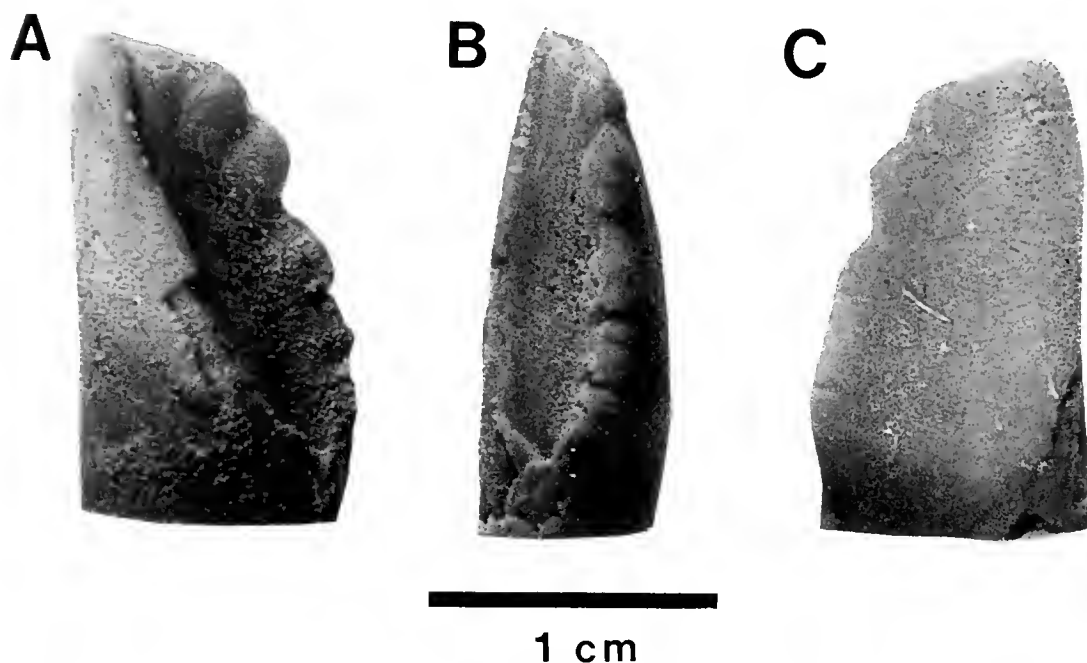
Fig. 4.—Proboscidea, indet., AK 95-1, right ?dI$_1$. A. Mesial view. B. Dorsal view. C. Lateral view.

C = A > E; B and D are much larger than A, C, or E. The inflated bases of cusps B and D fill the entire width of the stylar shelf. Cusps A and E are located, respectively, at the anterior and posterior corners of the stylar shelf. Cusp E is joined to the metacone by a posteriorly convex postmetacrista, but the preparacrista terminates just lingual to the base of cusp A. A short crest extends anterolingually from the small, central cusp C to the base of the paracone. The metacone is slightly higher than the paracone, and a straight centrocrista joins the two cusps. Both are inflated at their bases, as is the worn, crescentic protocone, which fills the entire lingual half of the tooth. A preprotocrista extends buccally from the protocone to the base of the paracone. The postprotocrista terminates at the base of the metacone in a small but distinct metaconule. There is a narrow anterior cingulum that extends from stylar cusp A to the lingual base of the protocone. The very narrow posterior cingulum is much shorter, extending from the metacone to the metaconule. There is no lingual or buccal cingulum, and no vestige of a hypocone. Wear

is confined to the apices of cusps and crests, where the relatively thick enamel is breached and dentine is exposed. Of the stylar cusps, only the largest, cusp D, shows wear.

Discussion.—The affinities of this unusual specimen are uncertain, but the five well-developed stylar cusps, the relative proportions of the metacone and paracone, and the absence of any vestige of a hypocone or lingual postcingulum are all consistent with its interpretation as a marsupial. It differs from didelphid marsupials in the presence of distinct, albeit small, pre- and postcingula. Among marsupials, AK 95-19 is most reminiscent of *Glasbius*, a bunodont genus from the Cretaceous of North America (e.g., Clemens, 1966), and *Chulpasia*, from the Paleocene of Peru (Crochet and Sigé, 1993), both of
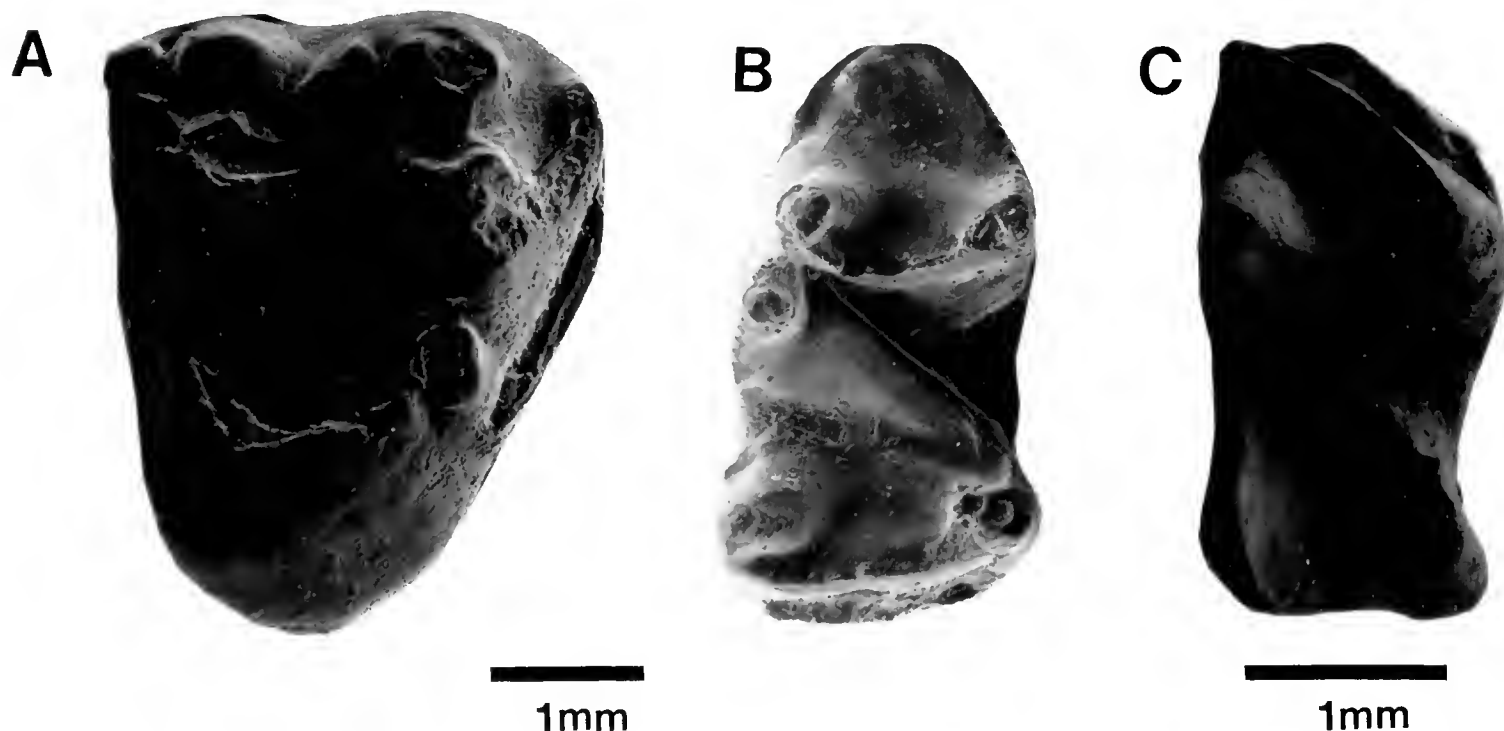
Fig. 5.—A. ?Marsupialia, gen. and sp. indet., AK 95-19, left M^1 or M^2. B. Mammalia, incertae sedis, genus and species 1, AK 95-20, right M$_1$ or M$_2$. C. Mammalia, incertae sedis, genus and species 2, AK 95-36, right M$_1$ or M$_2$.

which also possess inflated cusps, small pre- and postcingula, and similar patterns of stylar cusp development.

A number of eutherian mammal groups also are characterized by well-developed stylar cusps, but few of these possess more than three stylar cusps (parastyle, mesostyle, metastyle) (Crochet, 1980). Gheerbrant (1995) notes that some adapisoriculids (including the problematic *Garatherium* Crochet 1984) possess more numerous well-developed stylar cusps, but upper molars of adapisoriculids, like many primitive eutherians, are characterized by a much greater width-to-length ratio than AK 95-19. The enigmatic Plagiomenidae are another eutherian group whose upper molars are characterized by a plethora of stylar cusps (Russell et al., 1973; Rose, 1975; McKenna, 1990). Although AK 95-19 shows no special resemblance to known plagiomenid genera—in particular, it differs in the alignment and relative sizes of stylar cusps, and the absence of a protoconule—affinities with Plagiomenidae cannot be dismissed.

Order incertae sedis
New genus and species 1
(Fig. 5B)

Material.—AK 95-20, right M_1 or M_2, from Locality AK-32, Kartal Formation, Ankara, Turkey.

Description.—AK 95-20 is a high-cusped lower molar (length 3.5 mm, width 2.0 mm). The paraconid is reduced to a low paracristid which runs anteriorly and lingually from the protoconid and terminates just above the lingual end of the narrow anterior cingulum. The anterior cingulum continues around the buccal side of the tooth to the anterior base of the hypoconid. The paracristid is separated from the metaconid by a narrow valley. The metaconid is slightly higher than the protoconid; both are high, trenchant cusps, well separated but connected by a low postcristid. In profile, the protoconid is convex buccally and concave lingually, and the metaconid is convex lingually and concave buccally. A metastylid, nearly equal in height to the metaconid, is just posterior to the metaconid and very close to the lingual border of the tooth. The cristid obliqua runs from the anterior base of the metastylid posterobuccally to the hypoconid. The hypoconid is slightly lower than the tall, trenchant entoconid and is connected to the entoconid by a curving postcristid. There is a distinct entoconid notch between the metastylid and entoconid. There is no hypoconulid. There is a narrow, low posterior cingulum, but it is not continuous with the buccal cingulum, which terminates just anterior to the hypoconid.

Discussion.—The affinities of AK 95-20 are uncertain. The presence of a tall metastylid and the markedly lingual attachment of the cristid obliqua to the postvallid are similar to the three new species of ungulate from the Kartal Formation currently under study. However, it differs from those taxa, and

from other ungulates, in its high, trenchant cusps, which are well separated at their bases. In these features AK 95-20 resembles a number of tribosphenic mammals, including some tree shrews and proteutherians, but is distinct in its reduced paraconid and large metastylid.

Order incertae sedis
New genus and species 2
(Fig. 5C)

Material.—AK 95-36, right M_1 or M_2, Locality AK-1, Kartal Formation, Ankara, Turkey.

Description.—AK 95-36 is a high-crowned, tribosphenic lower molar (length 2.4 mm, width 1.3 mm). The trigonid is distinctly higher than the talonid, but similar in width. The paraconid is the lowest trigonid cusp. It is lingual in position and connected to the protoconid, the highest cusp, by a sharp crest which is interrupted midway by a notch. There is a deep notch between the base of the protoconid and the base of the metaconid. Both protoconid and metaconid are high and trenchant, but the metaconid is slightly lower than the protoconid. The cristid obliqua runs anteriorly from the relatively high hypoconid to meet the postvallid low and slightly buccal to the midline. A low postcristid runs down and lingually from the hypoconid to the midline of the tooth, then rises slightly to join a low hypoconulid. The hypoconulid is located in the posterolingual corner of the tooth, close to the entoconid. The entoconid is equal in height to the hypoconid. There is a short, strong anterior cingulum, but no buccal or posterior cingula.

Discussion.—This specimen shows general similarity to molars of a number of small tribosphenic mammals, including some marsupials, bats, insectivores, and tree shrews, especially in the relatively high trigonid, the trenchant cusps with well-defined shearing crests, and the relatively high paraconid. Like marsupials, the paraconid, metaconid, and entoconid are more or less lingually aligned, and the hypoconulid is closely appressed to the entoconid. The specimen differs from marsupials, however, in its more anteroposteriorly compressed trigonid and anteriorly convex paracristid. The lingual position of the hypoconulid is similar to marsupials, bats, and some tree shrews, but unlike most other insectivorous mammals.

This isolated tooth is remarkably similar to molars of the living tree shrew *Tupaia*. It also resembles YGSP 8090, an isolated tupaiid molar from the Miocene of Pakistan (Jacobs, 1980). Like these, AK 95-36 has a lingual hypoconulid, lacks a buccal cingulum, and has a paraconid–metaconid notch that is high relative to the entoconid notch. However, as noted by Jacobs (1980), none of these dental characters are unique to tupaiids, nor are they shared by all members of the family. The Kar-

tal specimen differs from tupaiids in the presence of a relatively broad anterior cingulum and in the slightly more lingual intersection of the cristid obliqua with the postvallid. Moreover, the geographic position of the Kartal specimen raises questions as to its possible tupaiid affinities—the Miocene tu-

paiid described by Jacobs is currently the westernmost occurrence of the group. Although additional material is necessary to identify the relationships of this specimen, it clearly represents a small mammal previously unknown from the Eocene of western Asia.

PALEOBIOGEOGRAPHY OF THE KARTAL VERTEBRATE FAUNA

Central Anatolia lies at the geographic crossroads of Asia, Europe, and Africa. It is situated near the intersection of two major plates, Eurasia to the north and Afro–Arabia to the south. Other tectonic units important in its early Tertiary history include the Sakarya continent (the location of the Kartal vertebrate localities) and the Anatolide/Tauride Platform (Fig. 6). The geological history of the region is quite complicated due to the shifting nature of plate boundaries and intervening microplates (Sengör and Yilmaz 1981; Görür et al., 1984; Sengör et al., 1984; Temiz et al., 1993), and there is uncertainty about the timing and position of plate contacts and the position and extent of hypothesized seas and emergent areas (see Robertson and Dixon, 1984, for review).

During much of the late Cretaceous through Eocene, the region witnessed convergence that resulted in the eventual closure of the Neo-Tethyan ocean branches north and south of the Anatolide/Tauride

Platform, and associated arc magmatism (Sengör and Yilmaz, 1981). The small Sakarya continent was isolated within the northern Neo-Tethyan branch until the late Cretaceous. Contact between the Sakarya continent and the Anatolide/Tauride Platform, along the Izmir–Ankara zone, probably occurred during the late Paleocene–early Eocene (e.g., Sengör and Yilmaz, 1981; Görür et al., 1984). The Anatolide/Tauride Platform appears to have shared a connection with the Apulian Platform to the west and perhaps remained attached to Africa through Sicily (Temiz et al., 1993). The southern Neo-Tethyan branch, between the Anatolide/Tauride Platform and the Afro–Arabian Platform, probably remained open until at least the late Eocene (Sengör and Yilmaz, 1981). The southern and northern Neo-Tethyan branches converged to the east of Central Anatolia, where emergent east–west trending island arcs (e.g., Dercourt et al., 1990) could have served as part of sweepstakes dispersal routes between Anatolia and eastern Asia. In sum, the presence of island arcs, numerous small plates, and theorized connections with emergent areas in almost all directions leave open the possibility that intercontinental mammalian dispersal by way of Central Anatolia could have occurred, at least intermittently, from the late Cretaceous through the Eocene.

The mammalian fauna recovered from Central Anatolia to date, including the Kartal fauna and the previous finds from Amasya (Sen and Heintz, 1979; Ducrocq and Sen, 1991), indicate faunal interchange with both Afro–Arabia and Europe. Taxa shared with Afro–Arabia include Embrithopoda and Proboscidea. The former are known from the late Eocene and early Oligocene of Africa (e.g., Tanner, 1978), whereas the African fossil record of the latter extends to the early or middle Eocene (Mahboubi et al., 1986). Haplobunodontid artiodactyls are common to the middle Eocene of Anatolia and the middle to late Eocene of Western Europe (e.g., Sudre, 1978; Ducrocq and Sen, 1991). Marsupials are now known from Anatolia (Kappelman et al., 1996), the early to late Eocene of Western Europe (e.g., Cro-
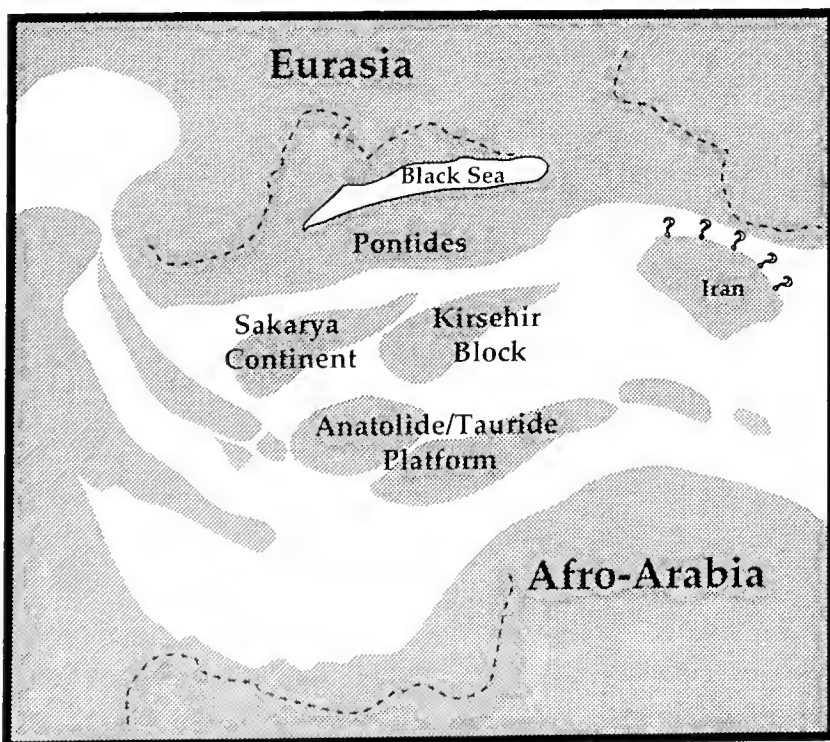

Fig. 6.—Cartoon reconstruction of Anatolia and vicinity in the early to middle Eocene, based on Sengör and Yilmaz (1981:fig. 6F) and Robertson and Dixon (1984:fig. 23f). Grey areas are continental blocks, white areas are ocean, dashed lines indicate some current coastlines.

chet, 1980), and the late Eocene (and, questionably, the early Eocene) of Afro–Arabia (Crochet, 1984; Simons and Bown, 1984; Crochet et al., 1992). However, based on our still very limited knowledge of the Anatolian fauna and our knowledge of regional paleogeography, we can neither pinpoint the most likely time, or times, of faunal exchange, nor eliminate the possibility of faunal contact between these regions at any time during the Eocene.

In contrast, the Kartal mammals show no affinities with eastern Asia forms, including the relatively well-known Indo–Pakistani Eocene mammals. This is particularly puzzling in light of the similarities between some eastern Asian and African forms in the late Eocene and early Oligocene (anthracotheriid artiodactyls, hystricognathous rodents, and anthropoid primates) (see Holroyd and Maas, 1994, for review). It raises the possibility that, despite the geographic potential for dispersal between eastern Asia and Afro–Arabia via Central Anatolia, faunal interchange occurred by way of a different, perhaps more southerly route (e.g., West, 1980). Another alternative is that the lack of similarity between eastern Asian and Turkish faunas might reflect age differences. The faunas from the Indian subcontinent, although generally referred to as middle Eocene in age, may in fact be early Eocene (e.g., Gingerich et al., 1990; Thewissen et al., 1987; Thewissen, 1990; Thewissen and Hussain, 1998) and thus older than the Kartal fauna, which, provisionally, appears to be early–middle Eocene in age (Kappelman et al., 1996). At present, however, the Anatolian mammalian fauna is still very poorly known. We expect that new finds from this intriguing geographic crossroads of East and West will clarify our understanding of Eocene circum-Tethyan biogeography.

ACKNOWLEDGMENTS

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THE ERGILIAN–SHANDGOLIAN (EOCENE–OLIGOCENE) TRANSITION IN THE ZAYSAN BASIN, KAZAKSTAN

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ABSTRACT

The Zaysan Basin, eastern Kazakstan, has a sedimentary section that represents much of Tertiary time, especially including strata that span the Eocene–Oligocene (Ergilian–Shandgolian) boundary. The upper part of the Aksyir svita produces mammals, including abundant rodents, that typically occur in the Ergilin–Dzo fauna of Mongolia and its correlates in Mongolia and China; it is thus considered Ergilian. Above the Aksyir is the Kusto svita, which is conformably overlain by the Buran svita; the latter two units are not everywhere separable on lithologic criteria. The Ergilian–Shandgolian transition is within this Kusto–Buran interval. *Cadurcodon ardynensis* occurs in this Kusto–Buran unit and in both Ergilian and Shandgolian deposits of Mongolia and China. Two quarry samples from the lower and middle parts of the Kusto–Buran unit have cylindrodont, zapodid, and cricetid rodents that are distinctly more derived than those from the upper Aksyir, but less derived than those from Shand Gol, Mongolia. A large quarry sample from a slightly younger level, clearly within the Buran "svita," has zapodids that are even more derived, along with the first occurrences of typical Shandgolian rodents: *Cricetops*, *Eucricetodon asiaticus*, Aplodontidae (*Prosciurus*), *Tsaganomys* (and/or includes *Cyclomylus*), castorids, and *Tataromys*.

ИЗМЕНЕНИЯ НА ГРАНИЦЕ ЭРГИЛИЯН-ШАНДГОЛИЯН (ЭОЦЕН-ОЛИГОЦЕН) В ЗАЙСАНСКОМ БАССЕЙНЕ КАЗАХСТАНА

РЕЗЮМЕ

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В Зайсанском бассейне восточного Казахстана имеет отложения, которые представляют весь третичный период, особенно выделяются пласты на границе раздела Эоцена—Олигоцена (Эргилиян—Шандголиян). В верхней части Аксыирской свиты находятся млекопитающие, включая обильный материал по грызунам, который обычно представлен в Эргилиян Дзо фауне Монголии и в коррелирующих слоях Китая. Выше Аксыирской свиты находится Кусто, которая перекрывает Буранскую свиту, две последних свиты не везде разделены по литологии. Эргилиян—Шандголиян изменения находятся в Кусто—Буранском интервале. В Монголии и Китае имеются находки Cadurcodon ardynensis из Кусто—Буранского блока в обоих Эргилиянских и Шандголиянских отложениях. В двух местонахождениях из нижней и средней части Кусто—Буранской свиты найдены цилиндродонты, заподиды, и крицетидные грызуны, которые значительно эволюционно продвинуты чем таковые из верхнего Аксыира, но в то же время менее развиты чем таковые из Шанда Гола. В другом обильном местонахождении которое относится к более раннему уровню, точнее к Буранской свите, имеются еще более эволюционно продвинуты заподиды, последние впервые встречаются вместе с типичными шандголинскими грызунами: Cricetops, Eucricetodon asiaticus, Aplodontidae (Prosciurus), Tsaganomys (и/или включая Cyclomylus), бобровые, и Tataromys.

INTRODUCTION

The present Lake Zaysan occupies a structural basin in the easternmost part of Kazakstan, near the northwestern corner of China and the western end of Mongolia (Fig. 1). This basin has been a site of deposition since the Late Cretaceous and has an Upper Cretaceous through Miocene sedimentary fill dominated by freshwater shales, siltstones, and fine sandstones deposited in and around ancestral Lake Zaysan (Borisov, 1963; Versilin et al., 1980). Especially in the southeastern half of the basin, Tertiary strata are exposed at many localities, usually along the courses of rivers that flow from surrounding mountains across the uplifted basin margins. These Tertiary strata produce rich assemblages of freshwater plants (charophytes), terrestrial plants (angiosperm leaves), invertebrates (ostracods, gastropods, and unionid bivalves), and vertebrates (amiid and teleost fishes, salamanders, turtles, crocodylians, birds, and mammals).

The Tertiary succession of the Zaysan Basin was summarized by Russell and Zhai (1987:158) as follows: "Perhaps nowhere in Asia within a restricted area is there a better sequence of continental Tertiary sediments than that found in the Zaysan Basin of eastern Kazakstan. Although dating is still uncertain for some deposits in the lower part of the Tertiary section, it is possible that all the epochs from the Late Cretaceous to the Quaternary are represented here. At least as concerns the Paleogene, the sequence is remarkably complete." Russell and Zhai (1987:159) presented diagrammatic maps and sections of several localities, including the most nearly complete section exposed at Kalmakpay Mountain (Fig. 3).

Our investigations during the past three years suggest that the section is not as complete as previously supposed (Fig. 2). The presence of Paleocene sediments is doubtful but cannot be completely

Fig. 1.—Map of Kazakstan, showing location of Lake Zaysan and Zaysan Basin. Rectangle indicates approximate extent of Figure 3.

ruled out; fossil plants suggest that Paleocene sediments may be present (Lucas et al., 1995), but no fossil mammals have been found that are older than middle Eocene. Middle Eocene (Irdinmanhan) mammalian faunas are well represented in the Chakpaktas and Obayla svitas, but as of yet we have no positive indication of Sharamurunian (late middle to early late Eocene) mammals. What the Zaysan Basin section does have is a relatively continuous section spanning the Ergilian (late Eocene) into the Shandgolian (early Oligocene). A sequence

of Ergilian to Shandgolian mammalian faunas occurs in the Aksyir svita and the overlying units which we refer to as the Kusto–Buran interval (Fig. 3–5).

DEFINITIONS

For purposes of this report we use the term "svita," the basic unit of stratigraphic analysis used by Soviet stratigraphers. Svitas are recognized not only by their lithologic characteristics, but also represent, at least in theory, isochronously-bounded time

EPOCH		LAND-MAMMAL "AGES"	SVITAS (BORISOV)
OLIGOCENE	L	TABENBULUKIAN?	Oshagande
			////////////////////
	E	SHANDGOLIAN	Buran
EOCENE	LATE	ERGILIAN	Kusto
			Aksyir
			Kyzylkain
	MIDDLE	SHARAMURUNIAN	////////////////////
		IRDINMANHAN	Sargamys
			Obayla
			Chakpaktas
			////////////////////

Fig. 2.—Tentative age assignments of Borisov's Paleogene svitas of the Zaysan Basin.

stratigraphic units recognized by their fossil content. Furthermore, the base of each svita is supposed to correspond to the initiation of a separate cycle of deposition. Each svita thus has lithologic, biochronologic, and genetic (sedimentologic) significance, so

the svita has no precise equivalent in Western stratigraphic theory and terminology.

As an appendix to their large volume on the Paleogene mammals and stratigraphy of Asia, Russell and Zhai (1987:411–436) documented and named a "sequence of mammal ages for the Paleogene of Asia" (Russell and Zhai, 1987:411). Herein we use the names applied by Russell and Zhai to those mammal ages that we recognize in the Zaysan Basin on the basis of the faunal characterizations provided by Russell and Zhai: Indinmanhan, Sharamurunian, Ergilian, and Shandgolian.

The Irdinmanhan Land Mammal Age was based on the Irdin Manha fauna of Nei Monggol, China (Russell and Zhai, 1987:415); their list of correlative faunas includes those of the "Chakpaktas, Obayla and Sargamys Svitas (Zaysan Depression)."

The fauna of the Shara Murun Formation of northern Nei Monggol, China, was the basis for "The Sharamurunian Land Mammal Age" (Russell and Zhai, 1987:419); among the faunas "considered
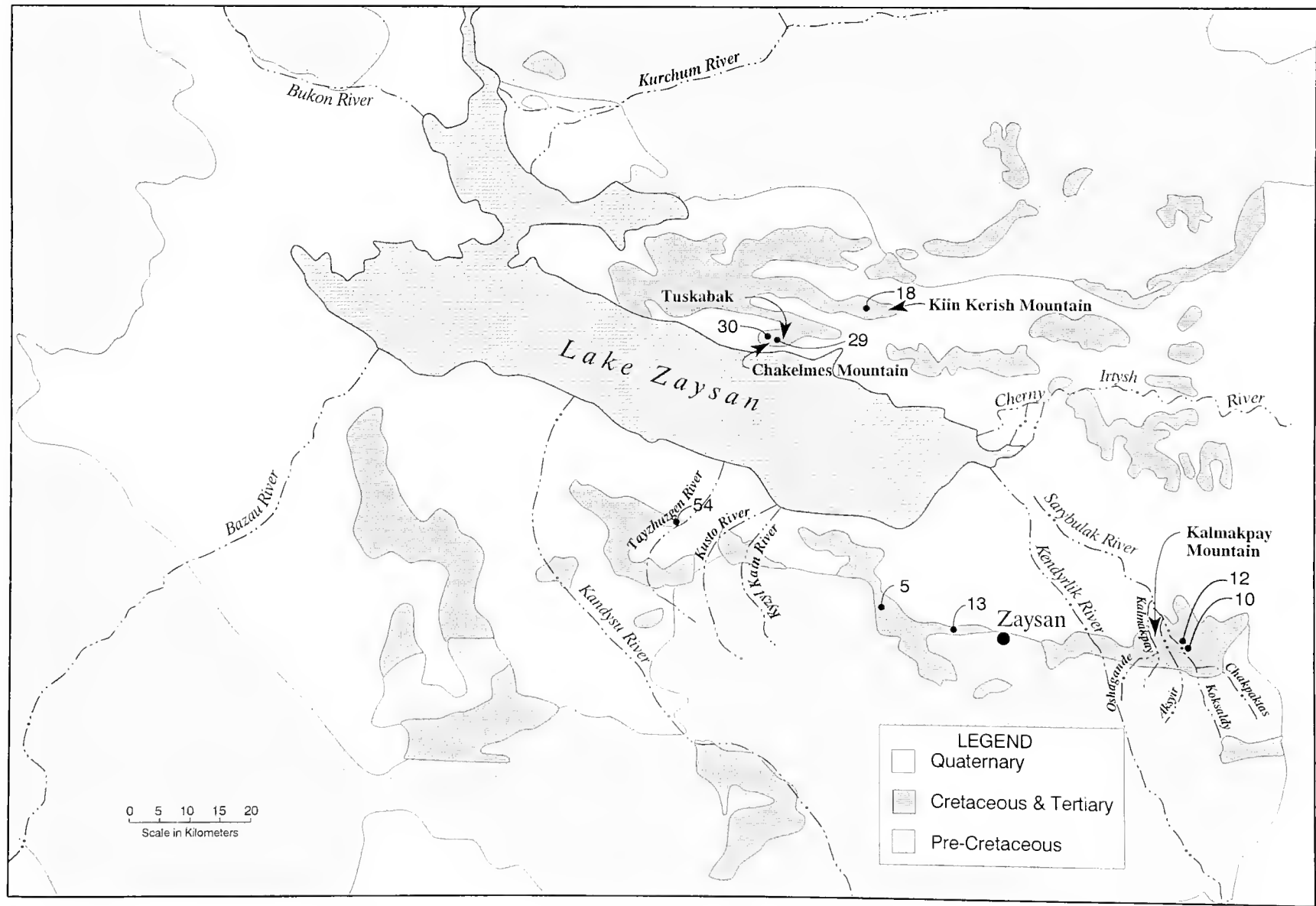

Fig. 3.—Generalized geological map of the Zaysan Basin in eastern Kazakstan showing distribution of fossil mammal localities in the Kusto–Buran interval discussed in the text and location of measured stratigraphic sections in Figure 2 (geology after Martinson and Kyansep-Romashkina, 1980).
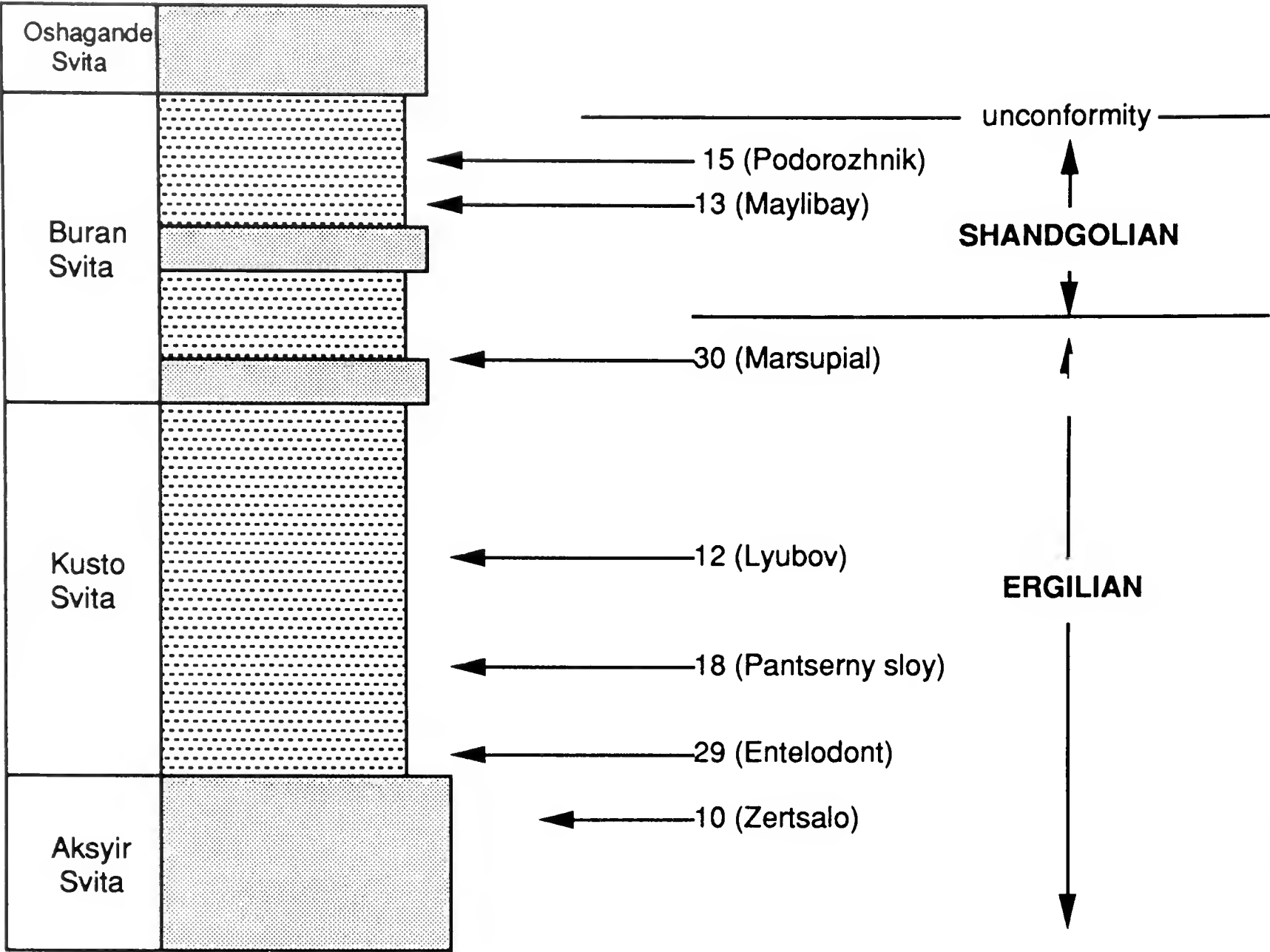
Fig. 4.—Summary of stratigraphic distribution of fossil localities in the Kusto–Buran interval in the Zaysan Basin.

tentatively as being of Sharamurunian age," Russell and Zhai (1987:419) listed the lower part of the Aksyir Svita of the Zaysan Basin.

The "Ergilian Land Mammal Age" was characterized by the Ergilin–Dzo fauna of Mongolia (Russell and Zhai, 1987:421); among the probable correlates, Russell and Zhai included the upper part of the Aksyir Svita of the Zaysan Basin.

"The Shandgolian Land Mammal Age" was based on the Shand–Gol fauna in Mongolia (Russell and Zhai, 1987:423); Russell and Zhai noted that the "Buran Svita of the Zaysan Basin" could be a correlate, but that the fossil material was inadequate for accurate correlation. Russell and Zhai's term Shandgolian is derived from "Shand–Gol," the transliteration used by Soviet workers for the de-

posits called Hsanda Gol Formation by Berkey and Granger (1923), and the fauna described in part by Matthew and Granger in several papers in the following two years (summarized by Mellett, 1968).

ABBREVIATIONS

AMNH refers to the American Museum of Natural History, New York, New York. KAN-Z refers to the Academy of Sciences of Kazakstan (Kazakskoi Akademiya Nauk), Institute of Zoology; specimen numbers with this prefix are in the collections of the Laboratory of Paleozoology of the Institute of Zoology, Academy of Sciences of Kazakstan, Almaty, Kazakstan. Land mammal age is sometimes abbreviated lma.
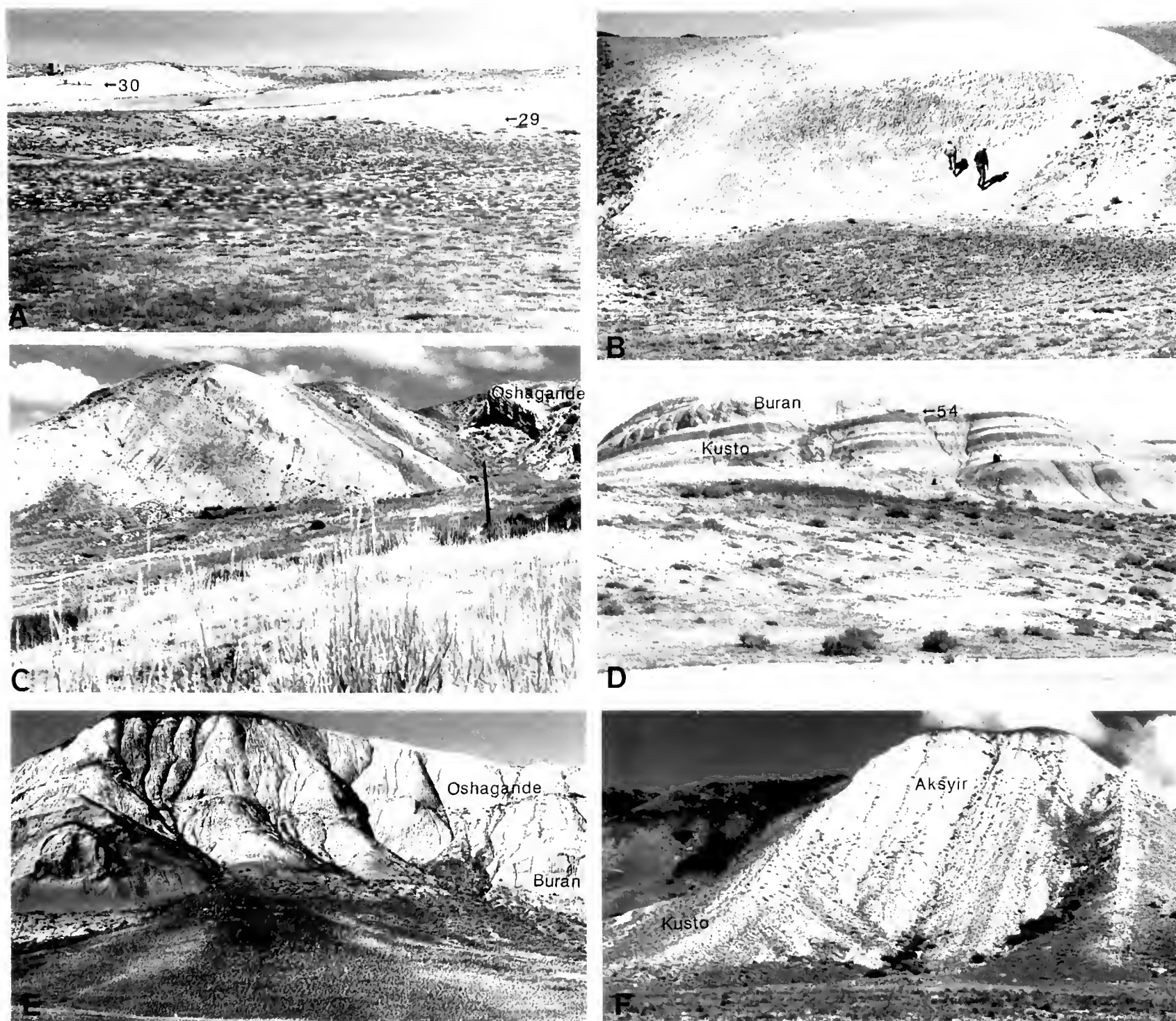
Fig. 5.—Selected outcrops of the Aksyir and Kusto–Buran interval in the Zaysan Basin. A. Tuskabak section showing locality K30 and horizon of locality K29 (actual locality is just to right of photograph). B. Drab brown mudstones of the Buran svita at the Maylibay locality (K13). C. Inclined strata of the Kusto–Buran interval underlying Oshagande svita sandstones on the south flank of the Aksyir River anticline. D. Green- and red-banded mudstones/shales of the Kusto svita overlain by tan mudstones and sandy mudstones of the Buran svita at the Talagay locality (K54) on the Tayzhuzgen River. Locality 54 is at the base of the Buran svita. E. Light-colored sandstones and siltstones of the Oshagande svita above Buran svita mudstones at the Kyzylkain River section B. F. Steeply dipping, light-colored sandstones and siltstones of the Aksyir svita overlain by poorly exposed green mudstones of the Kusto svita along the east bank of the Kusto River. This is in Borisov's (1963) type area of the Kusto svita. The top bed of the Aksyir svita is the last prominent, light-colored sandstone band just to the right of the word "Kusto" in the photograph.

LITHOSTRATIGRAPHY

Two lithostratigraphic (actually lithochronologic) schemes have been applied to Cenozoic strata of the Zaysan Basin. These schemes, of Lavrov and Yerofeyev (1958) and Borisov (1963), employ the Soviet stratigraphic term svita as the basic unit of lithostratigraphic analysis (see above).

In the Zaysan Basin, the units that are the focus of this report are the Aksyir, Kusto, and Buran svi-

tas. The term Aksyir svita was introduced by Borisov (1963) for a unit of siltstone/sandstone-dominated strata that forms one of the most distinctive and widespread lithostratigraphic units in the Zaysan Basin. The Aksyir svita can be easily recognized on the basis of lithologic characteristics, and could correspond closely to the concept of "formation" in Western stratigraphic terminology. Stra-

ta of the Aksyir svita are dominantly grayish yellow to yellowish orange siltstones and fine-grained sandstones that are typically laminated or ripple laminated. A few hummocky-bedded or trough-cross bedded sandstones are present and extensive bioturbation is common. Thin, laterally persistent beds of red, orange, and green shale in the Aksyir svita yield numerous charophytes and ostracods. Maximum observed thickness of the Aksyir svita is 123 m (on the Aksyir River), and the unit grades upward into the overlying Kusto svita. The cuestas, escarpments, and hogbacks formed by the relatively resistant Aksyir svita are present throughout the Zaysan Basin, and the Aksyir yields fossil mammals from numerous localities throughout its outcrop area.

Overlying the Aksyir svita is the Kusto svita and above that the Buran svita. Borisov (1963) also introduced these terms for a sequence of shale/mudstone-dominated strata in the Zaysan Basin to which he assigned a middle Oligocene age. Indeed, the Kusto and Buran svitas comprise a shale/mudstone-dominated package of strata as much as 140 m thick that crops out throughout the Zaysan Basin (Fig. 3–5). Kusto strata are mostly red and green variegated bentonitic shale, whereas Buran strata are mostly yellowish brown and gray variegated mudstones and siltstones (Fig. 3–5). Both units typically form slopes or valleys between ridges, cuestas, or hogbacks defended by the sandstone-dominated Aksyir (below) and Oshagande (above) svitas (Fig. 4, 5). The Kusto and Buran svitas are extremely fossiliferous, yielding numerous charophytes, megafossil plants, unionid bivalves, freshwater gastropods, and vertebrates (see articles in Martinson and Kyansep-Romashkina, 1980). Abundant ostracods and charophytes and the dominance of laterally continuous shale beds suggest that most of Kusto–Buran deposition took place in lacustrine or lacustrine margin environments (Martinson and Kyansep-Romashkina, 1980:fig. 22).

In their southwesternmost exposures in the Zaysan Basin, in the drainages of the Tayzhuzgen, Kusto, and Kyzylkain rivers (Fig. 5D–F), the Kusto and Buran svitas are readily distinguished from one another lithologically. Here, on the Kyzylkain River, the two svitas reach their maximum observed thickness of 97 m for the Kusto svita, and 42 m for the Buran svita. In the northwestern part of the basin, at Tuskabak (Fig. 5A) and Kiin Kerish, the two svitas cannot be readily separated lithologically and are much thinner, as they are also in the northeastern part of the basin at Ashutas Mountain, where their combined thickness is only 21.5 m. In the southeastern part of the Zaysan Basin, the combined Kusto and Buran svitas are relatively thick (Chakpaktas River, 66 m; Kalmakpay River, 52 m; Oshagande River, 34 m), but they cannot be separated lithologically. The section at Kalmakpay Mountain is a good example of this; here, 53.1 m of mostly grayish green shale represents the Kusto–Buran interval.

Two interpretations of the stratigraphy of the Kusto–Buran interval in the southeastern Zaysan Basin are possible: 1) the Buran svita is missing at the northern- and easternmost exposures, due either to not having been deposited or to having been beveled off by the unconformity at the base of the Oshagande svita; or 2) lithologies here that are typical of the Kusto svita grade laterally to the southwest into distinct Kusto and Buran svitas. Because no sites of Shandgolian age are known in the southeastern part of the basin, the first possibility seems more likely.

We do not recognize the Kusto and Buran svitas as lithostratigraphic units of formational rank—they cannot be distinguished or mapped on a lithologic basis throughout much of the Zaysan Basin. Instead, we unify these strata into a single, mappable lithostratigraphic unit of formational rank, which for purposes of this report, we refer to informally as the Kusto–Buran unit.

PALEONTOLOGY

The Aksyir svita is fossiliferous at virtually every place it is exposed, although the preponderance of the fossils are of aquatic vertebrates (fish, turtles, crocodylians). Several species of larger mammals are known from the Aksyir svita, but their fossils are relatively rare. Small mammals are very abundant at certain sites, particularly in the upper part of the Aksyir svita. Teeth of small mammals are very abundant at several levels at a locality called

Sunduk (Fig. 3, 4:site K10), an east–west trending anticline just east of where the Chakpaktas and Koksaldy rivers merge to form the Sarybulak River (Russell and Zhai, 1987:fig. 89). At least 20 m of upper Aksyir svita is exposed on the south limb of this anticline. Four fossil vertebrate localities occur at four levels in this sequence. Our locality K10, called Zertsalo ("looking glass") in the Russian literature and in Russell and Zhai (1987), has pro-

duced several thousand teeth of small mammals, predominantly rodents, through screen washing (the other localities are also productive, but the washed concentrate has not yet been sorted). The rodents from locality K10 are tentatively identified as follows: at least three species of Zapodidae (*Sinosminthus* sp., *Allosminthus*, cf. *A. ernos*, *Allosminthus* sp., and *Sinosminthus primiveris*), at least one species of Cricetidae (*Eucricetodon* sp.), one species of Cylindrodontidae (*Ardynomys* sp.), and at least one species of Ctenodactylidae (cf. *Karakoromys*). Site K10 also produces teeth that we refer to the small herpetotheriine didelphid marsupial *Asiadidelphis zaissanense* Gabunia, Shevyreva, and Gabunia, 1990, the holotype of which is from a nearby locality at a slightly lower stratigraphic level within the Aksyir svita.

Larger mammals reported by Gabunia (1977) from the upper part of the Aksyir svita are an indeterminate anthracothere, the anthracothere *Brachyodus*, and the leptomerycid *Archaeomeryx*. The presence of *Brachyodus*, otherwise known only from the Miocene, seems unlikely (Russell and Zhai, 1987). The holotype of *Zaisanamynodon borisovi* Belyayeva, 1971, is from the lower part of the Aksyir svita. This species of amynodont is now known to occur at several localities in Nei Monggol, China (Lucas and Emry, 1996a; Lucas et al., 1996). These occurrences include the Ulan Gochu Formation, which produces an extensive mammalian fauna of lagomorphs, rodents, an anagalid, a mesonychid, and brontotheriid and amynodontid perissodactyls. The Ulan Gochu Formation is among those listed by Russell and Zhai (1987:421) as providing fossil material that characterizes the Ergilian land mammal "age." At present, none of the mammalian fossils known from anywhere in the Aksyir svita suggest other than an Ergilian age for the entire Aksyir svita.

In the Kusto–Buran unit, which overlies the Aksyir, remains of larger mammals are much more abundant. The faunas from this interval are well represented at several localities in the Zaysan Basin (Russell and Zhai, 1987:284). Most important among them for this discussion are our localities K12, K13, K15, K18, K20, K29, K30, and K54 (Fig. 3, 4).

Perissodactyls and artiodactyls are predominant among the larger mammals. The holotype of *Amynodon tuskabakensis* Biryukov, 1963 (KAN-Z-57-2601/1419; Fig. 6A) is from the Kusto svita at Kiin Kerish (Biryukov, 1963). According to Lucas and Emry (1996a) this species is a synonym of *Cad-*

urcodon ardynensis, which has an Ergilian–Shandgolian distribution in China and Mongolia. The Kusto–Buran interval at Kalmakpay Mountain also produces *Cadurcodon ardynensis* (= *Cadurcodon zaisanensis* Belyaeva, 1962).

Brontotheres are not abundant in the Zaysan Basin, but do occur in the Aksyir and Kusto svitas. A brontothere maxillary fragment with P^4–M^2 (KAN-Z-369/MP-61; Fig. 6C) from Kiin Kerish is probably from the Kusto svita, but possibly from the Aksyir. It is a relatively small brontothere, but more derived than similar-sized genera of Irdinmanhan and Sharamurunian age such as *Microtitan* and *Protitan* in having a relatively molariform P^4 with a well-developed "tetartocone" (hypocone) (Granger and Gregory, 1943; Yanovskaya, 1980; Wang, 1982). In size and morphology, this maxillary most closely resembles *Epimanteoceras*. It is too small to represent *E. robustum* and a bit bigger than *E. formosus*; we refer to it as cf. *Epimanteoceras* sp. A brontothere molar (Fig. 6B) from site K29 places brontotheres in the lower part of the Kusto svita at Tuskabak.

Entelodon occurs in the Kusto svita at sites K12 and K29 (Fig. 3, 4, 7A; Emry et al., 1995). All well-dated records of *Entelodon* are Ergilian; the exceptions are a few records from what we believe are composites of Ergilian and Shandgolian assemblages, especially from the Turgay and Chelkar Teniz regions of north-central Kazakstan (Lucas and Emry, 1996a, 1996b). Dashzeveg (1993) indicates that the range of *Entelodon* terminates at the end of the Ergilian in Mongolia.

Musakulova (1963) reported *Gobiomeryx dubius* from the Kusto svita at Kiin Kerish. We have relocated the right dentary fragment on which Musakulova's report was based (KAN-Z-K-51 1262/1396, shown here as Fig. 7B), and concur that it does represent *Gobiomeryx dubius*, which, according to Russell and Zhai (1987), is known only from Ergilian strata.

All anthracothere specimens from the Kusto svita appear to represent a single taxon, too large and too derived (too selenodont) to be any of the common Asian Eocene anthracotheres such as *Anthracothema* or *Anthracokeryx*. The Zaysan anthracothere has a very long rostrum, and upper molars with broad, convex mesostyles (Fig. 7D). In the molar characters it is most similar to *Bothriodon*, *Aepinacodon*, and *Elomeryx*, but in the very elongate diastema anterior to the premolars in the lower jaw (Fig. 7C) it compares most closely with *Aepinacodon* of the North American Chadronian and earliest Orellan

Fig. 6.—Perissodactyl fossils from the Kusto svita of the Zaysan Basin. A. Holotype of *Amynodon tuskabakensis* (= *Cadurcodon ardynensis*), KAN-Z-57-2601/1419, from Kiin Kerish, probably locality K18 or K20. B. Right molar of unidentified brontothere, KAN-Z-K35(29)/4203, from Tuskabak, locality K29. C. Right maxillary fragment with P^4–M^2 of cf. *Epimanteoceras* sp., KAN-Z-369/MP-61, from Kiin Kerish, probably locality K18 or K20. A and C approximately ×1, B approximately ×0.5; scale bars in cm.

land mammal ages. We refer it tentatively to cf. *Aepinacodon* sp.

What appears to be one species of *Hyaenodon* occurs at both our sites K12 and K30. A right maxillary fragment with M^{1-2} from site K12 is very small. Its M^2 is apparently identical in size and morphology to AMNH 20364, a right M^2 of *Hyaenodon eminus* from Ardyn Obo. *Hyaenodon pervagus* from Shand Gol appears to be somewhat larger, although the known material does not allow direct comparison of corresponding parts.

Within the Kusto–Buran unit, sites K12 and K30 (Fig. 3, 4) appear to have identical faunas, both of small and larger mammals. Site K12 is in the southeastern end of the basin, just east of the Koksaldy River (UTM zone 45, 387305E, 5258046N), about 100 km to the southeast of site K30, which is on the northern side of Lake Zaysan at Tuskabak, near Chakelmes Mountain. Site K12 is in strata typical of the Kusto svita, whereas site K30 is in strata that, in lithologic characteristics, are more suggestive of the Buran svita. Russell and Zhai (1987:fig. 108)

published a diagrammatic section based on unpublished data provided to them by Borisov, which indicates Buran svita in the upper part of the Tuskabak section.

Both sites K12 and K30 have the zapodid genera *Heosminthus* and *Allosminthus*, and both also share another undescribed genus and species of zapodid, as well as an undescribed genus and species of cricetid. Site 30 has a cylindrodontid rodent that appears to represent a new genus and species; its cheek teeth are much higher crowned and have a simpler occlusal pattern than those of *Ardynomys*, but are somewhat lower crowned and less derived than those of *Cyclomylus* and *Tsaganomys*.

South of Lake Zaysan, in the southwestern outcrop area, where the Kusto–Buran interval is thickest, and where the Kusto and Buran are distinct from one another on lithologic criteria, several sites (Fig. 3, 4:sites K13, K15, K54) that are clearly in the Buran svita have a distinctly different small mammal fauna. Here, at site K15 (Podorozhnik), the rodents include the cylindrodonts *Tsaganomys* and/
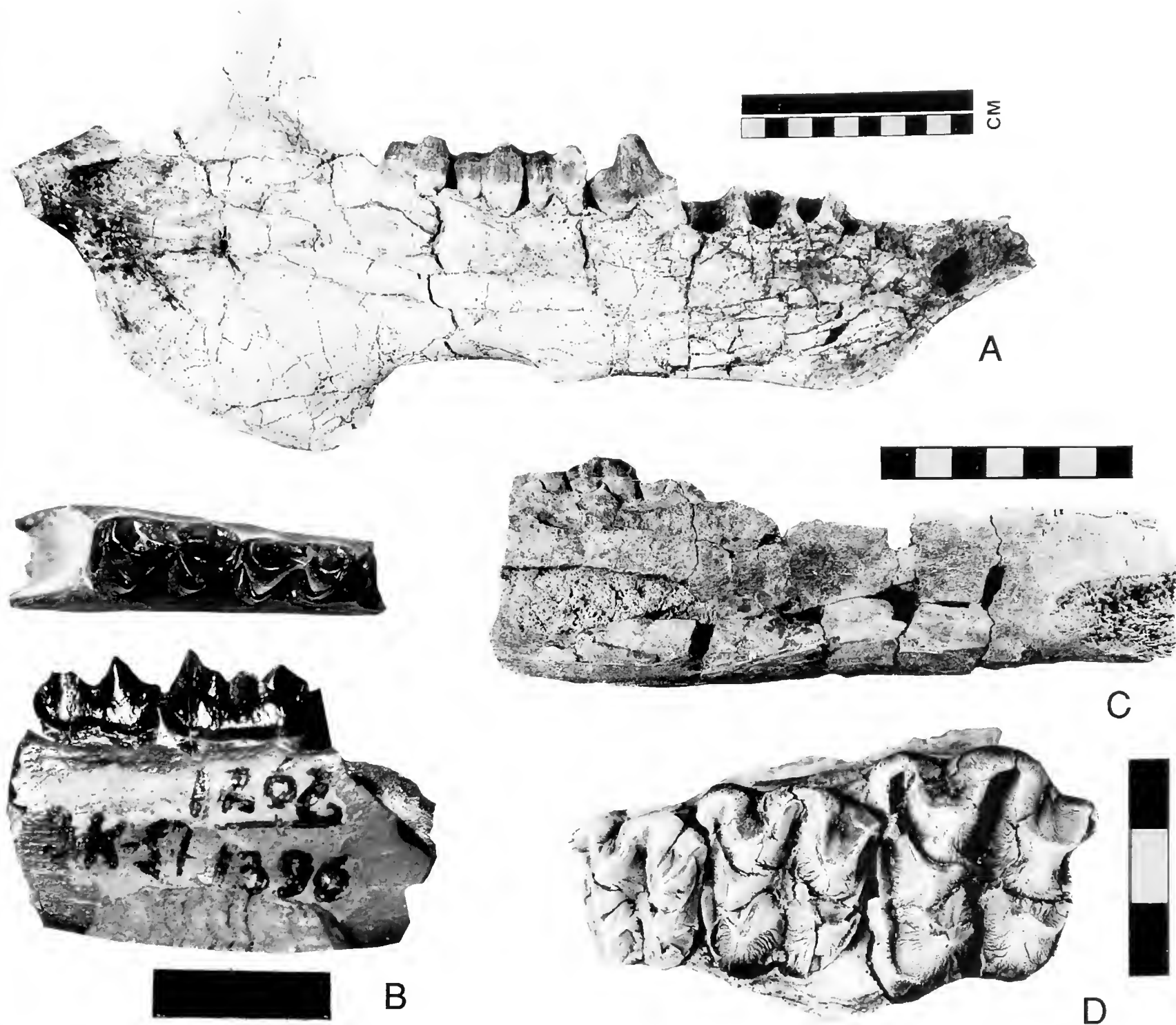
Fig. 7.—Artiodactyl fossils from the Kusto svita of the Zaysan Basin. A. Right dentary of *Entelodon gobiensis*, KAN-Z-K35(29)/3837, from Tuskabak, locality K29, approximately × 0.33. B. Right dentary fragment of *Gobiomeryx dubius* with M_{2-3}, KAN-Z-K-51-1262/1396, from Kiin Kerish, probably locality K18 or K20, in occlusal (above) and lingual (below) views, approximately × 2.5. C. Anterior part of left dentary of cf. *Aepinacodon* sp., KAN-Z-K35(18)/4213, from Kiin Kerish, locality K18, showing elongate diastema anterior to P_1, approximately × 0.5. D. Left maxillary fragment with M^{1-3} of cf. *Aepinacodon* sp., KAN-Z-K35(29)/4214, from Kiin Kerish, locality 18, approximately × 1. Scale bars in cm.

or *Cyclomylus* (Fig. 8A–C), and *Anomoemys lohiculus*; the cricetids *Cricetops* sp. (Fig. 8D, E) and *Eucricetodon asiaticus*; an aplodontid, *Prosciurus* cf. *P. ordosicus*; abundant ctenodactylids including *Tataromys* species (morphologies consistent with *T. plicidens*, *T. sigmodon*, *T. minor*) (Fig. 8F–H), *Karakoromys decessus*, *Karakoromys* sp., and *Bouno-*

mys sp.; abundant zapodids including *Parasminthus* species (morphologies consistent with *P. tangingoli*, *P. parvulus*, *P. asiaecentralis*), *Heosminthus* sp., and *Allosminthus* sp.; and castorids including *Steneofiber* cf. *S. butselensis* (Fig. 8I–K). At this site (K15) within the Buran svita, the fauna is clearly Shandgolian.
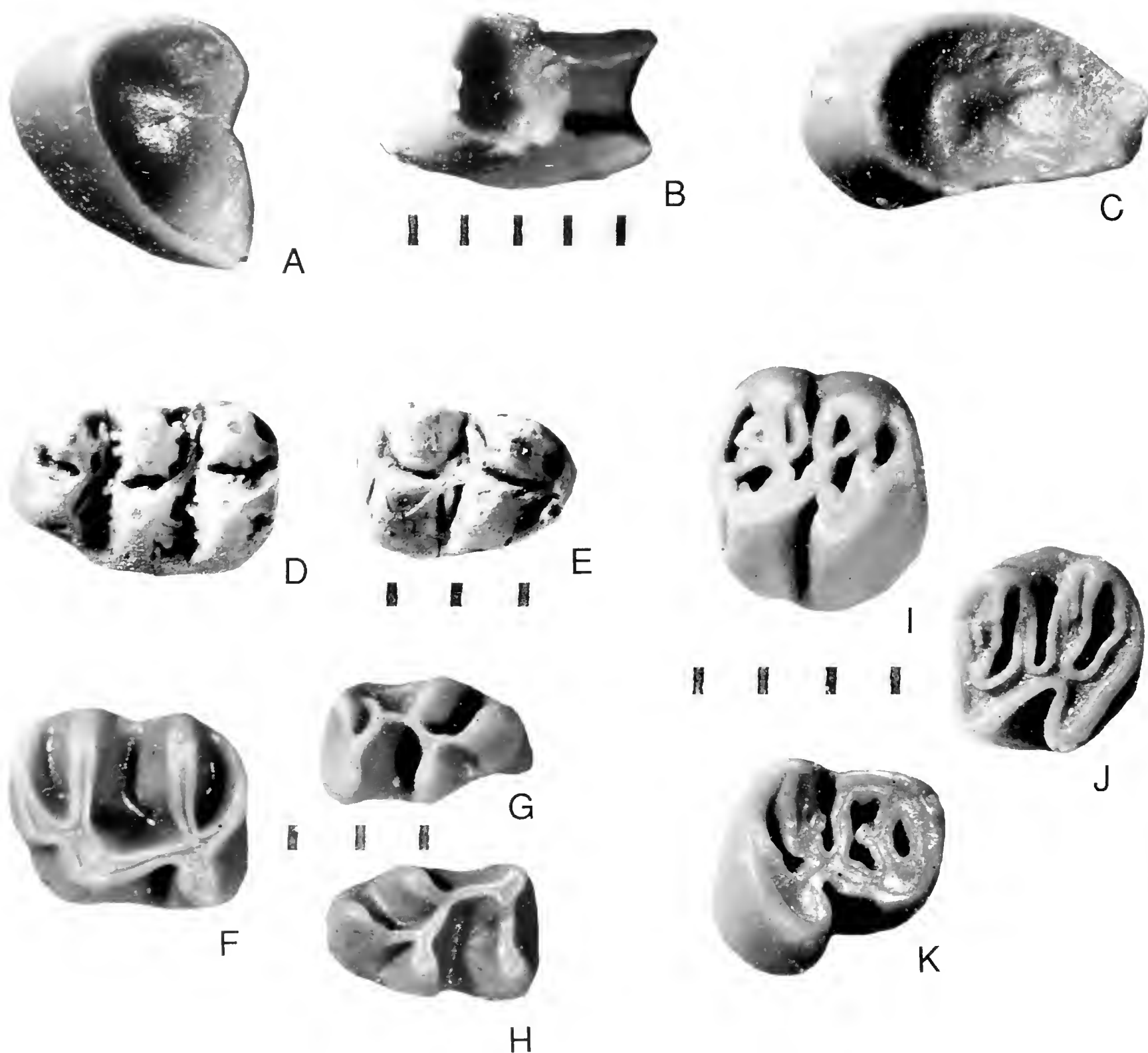
Fig. 8.—Representative Shandgolian rodents from Podorozhnik, locality K15, in the Buran svita. All numbers preceded by KAN-Z. A–C. *Tsaganomys* sp., K35(15)/424, K35(15)/425, and K35(15)/409, respectively. D, E. *Cricetops* sp., K35(15)/1837, K35(15)/1838, respectively. F–H. *Tataromys* sp., K35(15)/664, K35(15)/676, and K35(15)/681, respectively. I–K. Castoridae, cf. *Steneofiber* sp., K35(15)/1726, K35(15)/1730, and K35(15)/1734, respectively. A–C approximately × 7.5, D–K approximately × 9. Scale bars in mm.

EOCENE–OLIGOCENE BOUNDARY

For many years, Soviet vertebrate paleontologists considered the mammalian fossil assemblage of the Ergilin–Dzo svita in Mongolia to be characteristic of the early Oligocene (e.g., Yanovskaya et al., 1977). They based this conclusion in part on the well-established correlation of the Ergilin–Dzo mammals with those of the Chadronian land mammal "age" (lma) of western North America. Until recently, Western paleontologists regarded the Chadronian—for reasons of K/Ar geochronometry and magnetostratigraphy—as older than 36 or 37 Ma and thus assigned it to the early Oligocene. Recent agreement on an Eocene–Oligocene boundary stratotype section and point, however, moved that boundary upward to about 34 Ma (Premoli-Silva and Jenkins, 1993). New Ar/Ar ages from the Chadronian strata of Wyoming indicate the Chadronian lma also terminates at about 34 Ma, so the Eocene–

GENERA	ERGILIAN	SHANDGOLIAN
Amphechinus		
Tupaiodon		
Exallerix		
Desmatolagus		
Sinolagomys		
Ochotonolagus		
Ordolagus		
Procaprolagus		
Agispelagus		
Ardynomys	K	
Pseudocylindrodon		
Tsaganomys		B
Cyclomylus		B
Anomoemys		B
Prosciurus		B
Selenomys		
Tataromys		B
Karakoromys		B
Cricetops		B
Eucricetodon	K	B
Tachyoryctoides		B
Parasminthus		B
Mongolestes		
Metahaplodectes		
Pterodon		
Hyaenodon	K	B
Amphicticeps		
Palaeogale		
Plesictis		
Stenoplesictis		
Palaeoprionodon		
Nimravus		
Proailurus		
Amphicynodon		
Teleolophus		
Colodon		
Prohyracodon		
Ardynia		
Forstercooperia		
Paraceratherium		
Symphysorrachis		
Ronzotherium		
Allocerops		
Amynodon	K	
Cadurcodon	K	
"Gigantamynodon"		
Hypsamynodon		
Schizotherium		
Eomoropus		
Epimanteoceras	K	
Parabrontops		
Metatitan		
Titanodectes		
Embolotherium		
Eumeryx		
Pseudomeryx		
Miomeryx		
Lophiomeryx		
Palaeohypsodontus		
Eoentelodon		
Entelodon	K	
Bothriodon		
Ardynictis		
Didymoconus		

Fig. 9.—Summary of Dashzeveg's (1993) data on ranges of mammalian taxa in the Ergilian and Shandgolian of Mongolia. Occurrences of these taxa in the Zayzan basin are indicated by "K" for Kusto svita and "B" for Buran svita.

Oligocene boundary now correlates closely with the Chadronian–Orellan boundary (Prothero and Swisher, 1992).

Thus, Chadronian mammals are now considered late Eocene, as are correlative mammals in Asia, those of the Ergilin–Dzo svita. The oldest Oligocene mammal assemblage in Asia is well represented by the assemblage of the lower part of the Hsanda Gol svita, which immediately overlies the Ergilin–Dzo Formation in Mongolia. This repositioning of the Eocene–Oligocene boundary was not quickly accepted by Asian vertebrate paleontologists (cf. Wang, 1992; Dashzeveg, 1993), but is well accepted in the West (e.g., Berggren and Prothero, 1992; Ducrocq, 1993) and is followed here.

Two sets of lma nomenclature have been proposed for Asian fossil mammal assemblages that encompass the Eocene–Oligocene boundary. Li and Ting (1983:appendix 4) introduced "tentatively" a succession of "Chinese provincial ages" based on Paleogene mammals. They offered no explicit definitions of these "ages," only listing them and indicating which rock units and mammalian fossil assemblages corresponded to each "age." Two terms introduced by Li and Ting (1983) are relevant here, Ulangochuan and Houldjinian, considered by them to be of early and "middle" Oligocene age, respectively, but now known to straddle the Eocene–Oligocene boundary. The mammalian assemblage from the Ulan Gochu Formation in Nei Monggol, China, consists of less than 20 species, mostly brontotheres (Russell and Zhai, 1987:250). The Houldjin Formation is a conglomeratic unit in Nei Monggol with a low diversity assemblage of fossil mammals as well (less than ten species; Russell and Zhai, 1987:248). This assemblage appears to be a composite of middle Eocene–early Oligocene forms. Therefore, neither the Ulan Gochu or Houldjin fossil mammal assemblages seem particularly desirable as the basis of a land mammal "age."

Russell and Zhai (1987:421) introduced the term Ergilian lma for the mammalian fossil assemblage from the Ergilin–Dzo svita of Mongolia and assigned it an early Oligocene age. Russell and Zhai (1987) termed the middle Oligocene the Shandgolian based on the mammalian fossil assemblages (there are at least two: Mellett, 1968; Kowalski, 1974; McKenna, 1995) of the Shanda Gol Formation in Mongolia. Russell and Zhai (1987) offered no explicit definitions of these lmas, although they did give composite lists of the mammalian assemblages of the Ergilian and Shandgolian lmas. These lists, and Dashzeveg's (1993) plot of the actual

stratigraphic ranges of mammalian genera in the Er-gilin–Dzo and Hsanda Gol svitas (Fig. 9), provide the following criteria for differentiating Ergilian and Shandgolian mammal assemblages:

1. The last records of mesonychids and brontotheriids in Asia are of Ergilian age. The latter is particularly significant because brontotheriids are ubiquitous and abundant in Ergilian assemblages and conspicuously absent in Shandgolian assemblages.

2. A new rodent assemblage appears in the Shandgolian, especially *Tataromys*, *Tsaganomys* (and/or including *Cyclomylus*), aplodontids, castorids, *Cricetops*, and *Eucricetodon asiaticus*.

3. Three widespread taxa—the amynodontids

Zaisanamynodon (includes Gromova's [1954] nomen dubium *Gigantamynodon*) and *Cadurcodon*, and the entelodont *Entelodon*—may be restricted to the Ergilian. *Zaisanamynodon* records in China are of well-established Ergilian age (Lucas et al., 1996). Occurrences of both *Cadurcodon* and *Entelodon* are virtually all Ergilian; exceptions are a few records from what may be composites (especially those from the Turgay and Chelkar Teniz region of north-central Kazakstan) of Ergilian and Shandgolian fossil assemblages (Lucas and Emry, 1996a, 1996b).

4. Primitive indricotheres disappear at the end of the Ergilian and the giant indricothere *Paraceratherium* (= *Indricotherium*: Lucas and Sobus, 1989) appears in the Shandgolian.

ERGILIAN–SHANDGOLIAN BOUNDARY IN THE ZAYSAN BASIN

Borisov (1963, 1983) summarized previous Soviet opinions on the age of the Kusto–Buran interval in the Zaysan Basin, assigning it a "middle" Oligocene age. Subsequent Soviet workers (e.g., Akhmetiev et al., 1986; Yerbayeva, 1994; Shevyreva, 1995) have accepted this assignment, which is to correlate the Kusto–Buran interval to the "middle Oligocene" Hsanda Gol Formation of Mongolia. Russell and Zhai (1987) concluded that the Kusto and Buran svitas of the Zaysan Basin could be either early (= Ergilin–Dzo) or middle (= Hsanda Gol) Oligocene and noted that then-available material was inadequate for a more precise age determination.

Our data show that the Aksyir svita is Ergilian, and that the Ergilian–Shandgolian transition is within the Kusto–Buran interval. As noted, the upper part of the Aksyir svita is clearly Ergilian, and none of the fossil evidence suggests that the lower part is older than Ergilian. The Kusto svita has produced *Cadurcodon ardynensis* (= *Amynodon tuskabakensis*), Brontotheriidae (including the specimen here assigned to cf. *Epimanteoceras*), *Gobiomeryx dubius*, and *Entelodon gobiensis*, all of which are indicative of an Ergilian age.

Clearly, within the Aksyir through Kusto–Buran interval, the mammalian fauna changes from one that is typically Ergilian in the Aksyir to one that is clearly Shandgolian in beds that are distinctly Buran. Within the lower part of the Kusto–Buran unit, the faunas from sites K12, K29, and K30 have taxa that are either typical of Ergilian (*Cadurcodon ardynensis*, *Gobiomeryx dubius*, brontotheres), or, in the case of some of the rodents, seem to be advanced over their relatives in the underlying Aksyir svita, which is clearly Ergilian. Within the upper part of the Kusto–Buran unit, in deposits that are unambiguously Buran on lithologic criteria, the fauna contains *Cricetops*, *Eucricetodon asiaticus*, *Tataromys*, *Tsaganomys* and/or *Cyclomylus*, abundant castorids, and other taxa indicative of Shandgolian time. Several small mammal assemblages from several other levels within this Kusto–Buran unit have been collected by screen washing. Once these samples have been sorted and fully identified, we will have the unusual opportunity of observing the transition between two successive land mammal ages where there is abundant faunal information, rather than the hiatus that so often is the basis for defining and recognizing such a boundary.

ACKNOWLEDGMENTS

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OLIGOCENE STRATIGRAPHY, SEQUENCE STRATIGRAPHY, AND MAMMALIAN BIOCHRONOLOGY NORTH OF THE ARAL SEA, WESTERN KAZAKSTAN

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ABSTRACT

Oligocene marginal marine and nonmarine strata exposed north of the Aral Sea (Kumbulak Cliffs to Altyn Chokysu) comprise two unconformity-bounded sequences. The lower sequence rests disconformably on bentonitic marine shale of the upper Eocene–lower Oligocene Chegan Formation and consists of the Kutanbulak Formation, as much as 28 m of fine-grained quartzarenite, overlain conformably by the Chilikta Formation, as much as 23 m of shale and thinly interbedded shale/sandstone. The younger sequence begins with the Chagray Formation, as much as 33 m of micaceous sandstone that disconformably overlies the Chilikta. The Chagray grades upward into the Aral Formation, >24 m of calcareous shale and claystone. Stratigraphy, facies architecture, and paleontology support interpretation of the Kutanbulak and Chagray as lowstand and/or early transgressive systems tracts composed of river and delta deposits that infilled incised topography that previously developed during lowstand. Chilikta and Aral strata are late transgressive systems tracts and highstand systems tracts—mostly deposits of estuaries and lakes.

Homotaxis to marine strata on the Ustyurt Plateau and marine bivalves indicate the Chilikta is late Rupelian, and the Chagray is Chattian. The oldest Oligocene fossil mammals in these strata occur in the lower Chilikta—fragmentary remains of sirenians and of the giant rhinoceros *Paraceratherium*. This is the oldest local record of *Paraceratherium* and its only direct tie to marine biochronology. The classic mammal assemblage collected near Agyspe comes from the Aral Formation, as do recently collected micromammal assemblages from Altyn Chokysu and vicinity. Some Russian workers now regard these assemblages as of early Miocene age, but we identify them as late Oligocene because: 1) the Aral Formation is part of the same sequence as the Chattian Chagray Formation; 2) most of the genera and many of the species of Aral insectivores, lagomorphs, and rodents are known from the late Oligocene Tabenbulukian faunas of China and Mongolia; and 3) Aral megamammals include genera such as *Lophiomeryx*, *Prodremotherium*, *Protaceratherium*, *Aprotodon*, and *Paraceratherium* found in the European and/or Chinese late Oligocene. The Aral Formation fossil mammal assemblage represents one of the best documented late Oligocene mammal faunas known from Asia.

INTRODUCTION

Oligocene strata exposed north of the Aral Sea in western Kazakstan (Fig. 1) produce fossil mammals that include well-preserved specimens of the rhinoceros *Paraceratherium*, the largest land mammal to have ever lived. First collected in the 1930s, the fossil mammal localities north of the Aral Sea have only been organized stratigraphically in a general way. Prolific, recently collected micromammal localities (Bendukidze, 1993; Lopatin, 1994a, 1994b, 1995) from the Altyn Chokysu Plateau north of the Aral Sea have never been correlated directly to the previously collected, large-mammal-dominated sites along the northern shore of the Aral Sea at Perovsky

Bay east of Agyspe (Kazak: Akespe) (Fig. 2). Furthermore, global correlation of the fossil mammal localities near the Aral Sea, particularly their correlation to the Oligocene–Miocene boundary, has been debated (Lucas and Emry, 1995). Here, we present detailed physical stratigraphy and local correlation of the fossil mammal localities north of the Aral Sea (Fig. 5). We also interpret the sequence stratigraphy of these strata. We then review the composition and correlation of the fossil mammal assemblages. We conclude by discussing their correlation to other Eurasian fossil mammals and to the Oligocene–Miocene boundary.

LOCATION

The area north of the Aral Sea is referred to by Soviet geologists as the Severnoye Priaralye, literally the northern in-front-of-the-Aral, here referred to as the Northern Priaral. Fossil mammal localities here occur in three distinct outcrop areas (Fig. 2):

1. Altyn Chokysu (Fig. 2) is a long, southwest–northeast-trending plateau about 20 km north–northwest of Saksaulskoye, the nearest city on the main trans-Kazakstan railway. Paleogene strata crop out on the southeastern and eastern escarpments of this plateau as continuous exposures for at least 15 km (Fig. 6). We measured four stratigraphic sections that encompass six fossil vertebrate localities and three fossil plant localities at Altyn Chokysu (Fig. 5, sections D–F, H; Table 1).

2. Aktau Mountain (Fig. 2, 8B) is a small conical hill about 20 km northwest of Altyn Chokysu. We measured a section here (Fig. 5:section G) to encompass the fossil mammal locality Bendukidze (1993) referred to as "Akotau" (an incorrect transliteration of the Kazak word Aktau, which means white mountain).

3. The Kumbulak Cliffs (Fig. 2, 7) ring the northern shore of the Aral Sea along Perovsky Bay east of the village of Agyspe. The classic *Paraceratherium* quarry worked by the Soviet Academy of Sciences in the 1930s is here (Orlov, 1939), as is a locality recently collected by Bayshashov (1993). Glikman (1964) described fossil sharks from this area, and several plant localities also are present (Zhilin, 1989). We measured three stratigraphic sections at the Kumbulak Cliffs (Fig. 5:sections A–C).

PREVIOUS STUDIES

Geological observations of Tertiary strata in the Northern Priaral date back to Neshel (1847), an engineer who identified Tertiary sands of marine origin in the Altyn Chokysu area. Fossils collected by K. Oklandnyy in 1860 were studied by Gelmersen (1868, 1879) and Romanovskiy (1878, 1884, 1890), leading to the first stratigraphic scheme for the Northern Priaral. The geological map of Turkestan (Romanovskiy and Mushketov, 1884) employed this scheme, which assigned a Quaternary age to the sands exposed at Altyn Chokysu. In contrast, Mushketov (1886, 1908) identified the strata at Altyn Chokysu as Tertiary surrounded by Quaternary sediments.

The explorer Berg (1908) published his classic monograph on the Aral Sea in which he described the Aral basin and the geology of its shores. Berg presented a new stratigraphic scheme in which he identified (ascending order): 1) "nummulitic" strata of middle Eocene age, 2) quartzitic sands of late Eocene age, 3) gypsiferous clays with molluscs (Chegan Formation of current usage) of Oligocene age, and 4) Aquitanian sands.

Bogachev (1909) first recognized the presence of beds (Aral Formation of current usage) with the bivalve *Corbula* at Altyn Chokysu and correlated them with the Solenov (Oligocene) horizon on the Ustyurt Plateau to the southwest. Mikhaylovskiy (1909) named *Corbula helmerseni* for specimens from Ustyurt and considered it to be of early Miocene age. Biostratigraphic correlation based on *Cor-*

bula helmerseni became the rationale for subsequent recognition in the Northern Priaral of the Aral svita (Yanshin, 1940, 1953), Aral stage (Zhizhchenko, 1940; Petrushevskiy, 1946; Yanshin, 1949), Aralian beds (Vakhrameyev, 1949) or Corbulian beds (Vyalov, 1937, 1945).

Neustruyev (1912), Krasheninnikov (1925), and Kassin (1937, 1947) concluded that the Tertiary sands of the Northern Priaral were deposited by a Siberian river that flowed through the Turgay region of north-central Kazakstan to the Aral and Caspian basins. The paleontologist A. K. Alekseyev collected fossils in the Northern Priaral in 1930–1931. Alekseyev (1936, 1937, 1945) applied the name Saksaul svita, which he regarded as of middle Eocene age, to the sands and clays exposed near Saksaulskoye station.

Near Agyspe, Alekseyev discovered fossil bones in clays and limy clays with *Corbula helmerseni* that he considered to be of late Oligocene age. Working for the Soviet Academy of Sciences, M. G. Prokhorov excavated these localities in 1932–1933, followed by Yu. Orlov in 1936 and 1938. These fossils were described primarily by Prokhorov (1934a, 1934b), Borisyak (1936, 1939, 1944), Borisyak et al. (1938), Argyropulo (1939a, 1939b, 1940), Orlov (1939), Tugarinov (1940), and Khozatskiy (1945). These authors considered the vertebrate fossils to be of late Oligocene age, well reflected in some of the names they proposed, such as *Anas oligocaena*, a fossil duck named by Tugar-

Fig. 1.—Map of Kazakstan showing location of study area north of the Aral Sea.

inov (1940). Most vertebrate paleontologists have long accepted a late Oligocene age for the fossil mammal assemblage collected near Agyspe (e.g., Borisyak and Belyayeva, 1948; Thenius, 1959; Russell and Zhai, 1987), although some have been less certain, terming them "Oligocene–Miocene" (Savage and Russell, 1983).

The discovery of fossil mammals in the Northern Priaral was soon followed by collections of fossil plants, beginning with work on the Sarybulak Plateau near Chokysu station by Poyarkova (1935),

who assigned the floras an Aquitanian age. The paleobotanical work of Rayushkina, Zhilin, and Akhmetiev followed (see summaries by Zhilin, 1989, and Andreyev, 1991).

In 1937–1939, A. L. Yanshin directed extensive work in the Northern Priaral by geologists of the Geological Institute of the Soviet Academy of Sciences. They developed a new and more detailed stratigraphic scheme for the lower part of the section (ascending order): 1) Tasaran svita, gray shales of middle and early late Eocene age; 2) Saksaul
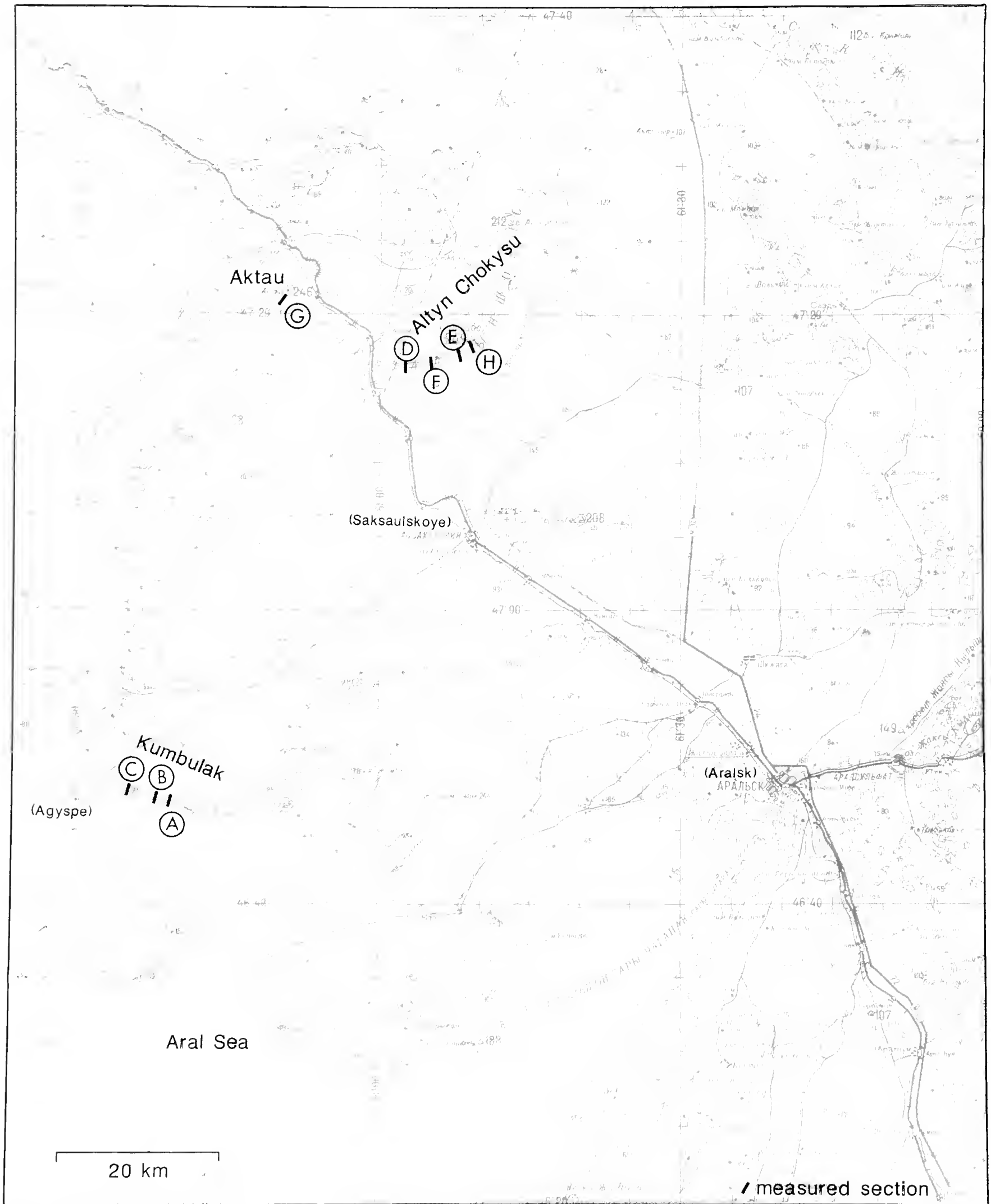
Fig. 2.—Topographic map of the study area (from Aralsk, 1:500,000 quadrangle) showing locations of measured stratigraphic sections.

Table 1.—*Oligocene fossil plant and vertebrate localities north of the Aral Sea (Fig. 5).*

Locality no.	UTM	Stratigraphic unit	Fossils	Principal references
1	41319027E 5184292N	Chilikta Formation (Fig. 3, sec. A, unit 10)	shark teeth	Glikman (1964)
2	41316737E 5185226N	Aral Formation (Fig. 3, sec. B, units 16, 17)	mammals	see Russell and Zhai (1987)
3	413169664E 5185191N	Chagray Formation (Fig. 3, sec. B, unit 5)	shark teeth	Glikman (1964)
4	41315113E 5186634N	Aral Formation (Fig. 3, sec. C, unit 26)	mammals	Bayshashov (1993)
5	41314754E 5186349N	Chilikta Formation (Fig. 3, sec. C, unit 11)	plants (*Taxodium*)	Akhmetiev (1994)
6	41350801E 5237784N	Aral Formation (Fig. 3, sec. D, unit 46)	*Paraceratherium*	this paper
7	41352892E 5237956N	Aral Formation (Fig. 3, sec. D, unit 45)	mammals	Lopatin (1994*b*)
8	41352892E 5237956N	Aral Formation (Fig. 3, sec. D, unit 25–28)	mammals	Lopatin (1994*b*)
9	41352892E 5237956N	Aral Formation (Fig. 3, sec. D, unit 24)	mammals	Lopatin (1994*b*)
10	41350881E 5237470N	Chilikta Formation (Fig. 3, sec. D, unit 8)	plants (AC V)	Andreyev (1991)
11	41357557E 5239091N	Aral Formation (Fig. 3, sec. E, unit 51)	mammals (Chokysu)	Bendukidze (1993)
12	413577371E 5238795N	Chilikta Formation (Fig. 3, sec. E, unit 23)	mammals	Lucas and Emry (1996*a*)
13	41352089E 5237703N	Chilikta Formation (Fig. 3, sec. F, unit 10)	plants (AC II) (*Nelumbo* lens)	Snigirevskaya and Zhilin (1974)
14	41360847E 524057N	Chilikta Formation (Fig. 3, sec. H, unit 4)	plants (Sary Oba—AC VI)	Andreyev (1991)
15	41336840E 5247342N	Aral Formation (Fig. 3, sec. G, unit 13)	mammals ("Akotau")	Bendukidze (1993)

svita, white quartzose sands of late Eocene age; and 3) Chegan svita (of Yanshin, 1940), green shales with limy concretions of late Eocene–early Oligocene age. This stratigraphy was mapped at a scale of 1:420,000 (Yanshin, 1939).

Petrushevskiy (1946) published a geological map of the eastern part of the Northern Priaral at a scale of 1:1,000,000 on which he assigned the strata at Altyn Chokysu to the lower–middle Eocene. Vakhrameyev (1949; also see Formozova, 1951) named two middle Oligocene svitas (Kutanbulak and Chilikta) and two of late Oligocene age (Dzharsiklich and Chagray) in this area.

In his monograph on the geology of the Northern Priaral, Yanshin (1953) presented a comprehensive stratigraphic scheme for the Cretaceous and Cenozoic that took into account prior paleontological work. He considered the section north of Saksaulskaya station to be the stratotype of the Tasaran, Saksaul, and Chegan svitas of Paleogene age.

Ovechkin (1954) wrote a monograph on the megainvertebrate fossil assemblages of the Chegan svita in which he recognized four zones of late Eocene

age (ascending order): 1) *Vermetus* spp. zone, 2) *Turritella* spp. zone, 3) *Pholas scutata/Cultellus grignonensis* zone, and 4) *Pinna lebedevi* zone. However, based on foraminiferans, Bondaryeva (1955) placed the Eocene–Oligocene boundary in the *Turritella* spp. zone of Ovechkin, thus assigning most of the Chegan svita an early Oligocene age.

Bublis et al. (1959) published a geologic map at the scale of 1:200,000 in which they identified the continental deposits at Altyn Chokysu as the Kutanbulak, Chilikta, and Chagray svitas. However, Bronevoy (1965) and Snigirevskaya and Zhilin (1974) assigned these strata to a single, Chagray svita. The latter authors described an extensive flora from these strata. The geologic map (scale 1: 500,000) of Bolukov et al. (1959) for this region identified the stratigraphic succession at Altyn Chokysu as (ascending): Saksaul svita (marine late Eocene), Chegan svita (marine early Oligocene), Turgay svita (continental Oligocene), and Aral svita (continental Oligocene).

Most contemporaneous and subsequent maps of the 1950s and 1960s contributed nothing new to our

understanding of Tertiary stratigraphy and age relationships in the Northern Priaral (e.g., Bondaryeva, 1955, 1964; Bondaryeva and Samodurov, 1961; Mironova et al., 1962; Kiryukhin and Nikolayeva, 1967). Ovechkin (1962) correlated the Priaral Tertiary to the Turgay Tertiary, and most workers (e.g., Lavrov, 1951, 1959; Bronevoy and Bryzzheva, 1963; Boytsova et al., 1964; Bronevoy, 1965; Bronevoy and Kiryukhin, 1966; Buklin and Mukhin, 1967; Buklin and Belyankin, 1972) employed Yanshin's stratigraphic scheme. Lavrov (1959, 1979), however, assigned a Miocene age to the Aral Formation and envisioned it as part of a widespread lacustrine episode throughout Kazakstan.

New stratigraphic work published in the 1960s and 1970s refined the currently employed lithostratigraphy of Tertiary strata in the Northern Priaral and advocated some new age assignments (Bronevoy and Kiryukhin, 1966; Bronevoy and Zhilin, 1967; Bronevoy et al., 1967a, 1967b; Velikiy et al., 1969; Bulekbayev et al., 1970; Velikiy and Miletskiy, 1971; Buklin and Belyankin, 1972; Lavrov et al., 1978; Voznesenskiy, 1978). Thus, the marine Chegan svita of late Eocene or late Eocene–early Oligocene age is overlain by the Oligocene Kutanbulak, Chilikta, and Chagray svitas capped by the Oligo–Miocene (Voznesenskiy, 1978) or Miocene (Lavrov et al., 1978) Aral svita. Voznesenskiy's (1978) monograph was particularly important because it provided a lithostratigraphically-based correlation of the Priaral section to the genetically related, much thicker and more marine-dominated section to the west on the Ustyurt Plateau (Fig. 3).

The assignment of a Miocene age to the Aral Formation was developed further in the 1980s by a variety of Russian paleontologists who collected fossil plants and vertebrates in the Northern Priaral. Articles in Akhmetiev and Sychevskaya (1994) and abstracts in Tleuberdina and Akhmetiev (1994) summarize this recent work well. Particularly important is Bendukidze's (1993) monograph on the micromammal assemblages of the Aral Formation, especially those from the Altyn Chokysu Plateau, and Lopatin's (1994a, 1994b, 1995) preliminary reports on micromammal assemblages of the same provenance.

LITHOSTRATIGRAPHY

We studied five lithostratigraphic units (formations, formerly svitas) of Paleogene age that crop out in the Altyn Chokysu–Kumbulak region (ascending order): Chegan, Kutanbulak, Chilikta, Chagray, and Aral (Fig. 4). Formerly these units were termed svitas, a Soviet stratigraphic subdivision that refers to a lithologically distinctive unit with isochronous boundaries that represents a particular cycle or phase of deposition. However, the five formations recognized here are mappable units that can be distinguished solely on lithologic criteria, so they can be properly referred to as formations (Akhmetiev, 1994).

CHEGAN FORMATION

The oldest Paleogene strata exposed north of the Aral Sea that we measured belong to the Chegan Formation (Fig. 5, 6A, 7B). Chegan strata are mostly yellowish green, bentonitic marine shale that contains brownish gray and pale yellowish brown sideritic nodules. Fossils of dinocysts, turritellid gastropods, marine bivalves, and nautiloids establish the marine origin and age of the Chegan Formation as late Eocene–early Oligocene (see Akhmetiev and Zaporozhets, 1992, and references cited above). Total thickness of the Chegan Formation in this area is at least 56 m, but we made no effort to study this unit in detail. No fossil vertebrates are known from the Chegan Formation in the study area.

KUTANBULAK FORMATION

The Kutanbulak Formation ranges in thickness from 0 to 28.3 m in the study area. It disconformably overlies the Chegan Formation and is conformably overlain by the Chilikta Formation (Fig. 5, 6A, 7B, 8A). Kutanbulak strata are almost entirely sandstone; sandy siltstone is rare, and finer grained clastics are essentially absent. Yellowish gray, grayish yellow, dark yellowish orange, and yellowish brown are the dominant colors due to the ferruginous (limonitic) nature of these sandstones, which are mostly very fine- to fine-grained quartzarenites. Bedforms are mostly laminations, ripple laminations, and trough crossbedding. In the Kumbulak Cliffs, steeply dipping delta foresets are common (Fig. 5, 6B, 7A). No fossil vertebrates are known from the Kutanbulak Formation in the study area, but it has produced fossil plants from one locality (Rayushkina, 1977).

CHILIKTA FORMATION

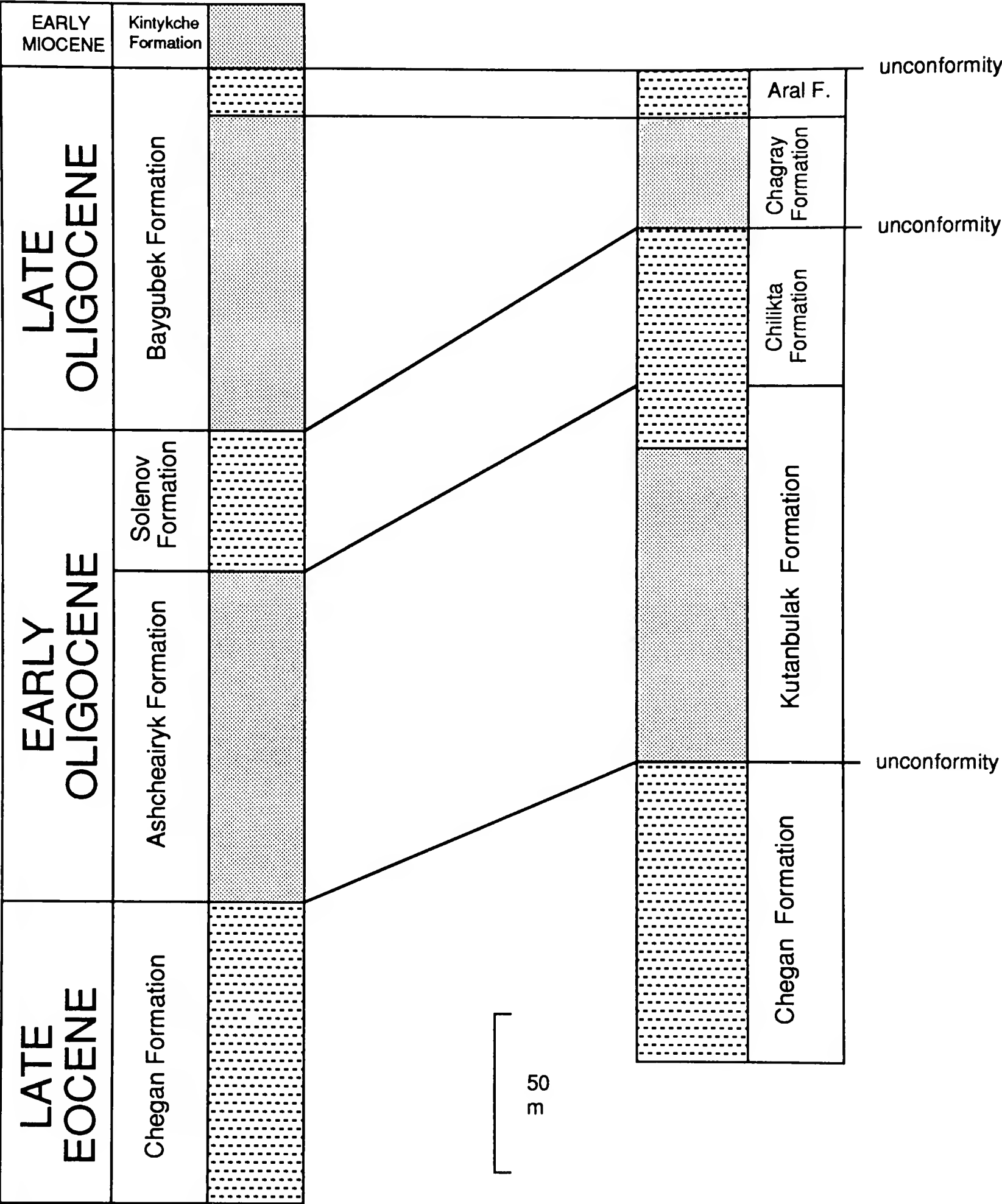The Chilikta Formation conformably overlies the Kutanbulak Formation and is disconformably over-

Fig. 3.—Correlation of Eocene–Miocene strata between the Northern Ustyurt and Northern Priaral (modified from Voznesenskiy, 1978).
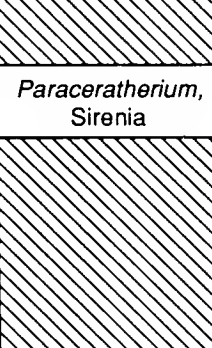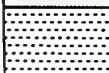
LITH.	STRAT. UNIT	DOMINANT LITHOLOGY	MAX. THICK.	FOSSIL MAMMALS
	Aral Formation	green claystone and shale	24.2 m	Aral local fauna
	Chagray Formation	yellowish gray sandstone	32.9 m	
	Chilikta Formation	pinkish gray shale and sandstone	22.7 m	*Paraceratherium*, Sirenia
	Kutanbulak Formation	yellowish gray sandstone	28.3 m	
	Chegan Formation	yellowish green bentonitic shale	56 m	

Fig. 4.—Summary of Oligocene stratigraphic units exposed in the Northern Priaral.

lain by the Chagray Formation (Fig. 5, 6A, 7B, 8A). Most of the Chilikta, which ranges in thickness from 8.7 to 22.7 m, consists of shale or thinly interbedded sandstone and shale. Typical colors of the shale are pinkish gray, grayish orange pink, pale yellowish brown, and olive brown. Chilikta sandstones resemble Kutanbulak sandstones in being mostly yellowish brown and yellowish orange, very fine- to fine-grained, ferruginous (limonitic) quartzarenite, and they tend to be micaceous (muscoviterich). Trough crossbeds are the dominant bedform.

Measured sections demonstrate that sandstones dominate the lower part of the Chilikta Formation, whereas shales dominate its upper part (Fig. 5). Sandstones of the lower part of the Chilikta produce selachian teeth (Glikman, 1964). One locality in the upper part of the Chilikta Formation yielded a sirenian rib fragment and tooth fragments of the rhinoceros *Paraceratherium* (Lucas and Emry, 1996a). Shales from the upper part of the formation produce a diverse and prolific paleoflora preserved as leaf compressions and impressions (e.g., Zhilin, 1989; Andreyev, 1991). A single bed at Altyn Chokysu produces ostracods (unstudied) and charophytes (Nikolskaya, 1977, 1988).

CHAGRAY FORMATION

The Chagray Formation disconformably overlies the Chilikta Formation and is conformably overlain by the Aral Formation (Fig. 5, 6, 7, 8A). Chagray thickness ranges from 7.2 to 32.9 m, and the formation is almost entirely sandstone. These sandstones are characteristically very micaceous, and we pick the base of the Chagray Formation at the first micaceous sandstone above the highest shale of typical Chilikta lithology. Chagray sandstones are yellowish gray, greenish yellow, yellowish orange, and yellowish brown, very fine- to fine-grained, ferruginous (limonitic) quartzarenites and micaceous litharenites. Some sandstones are clayey, and trough crossbeds are the prevalent bedform, although some beds are laminated, ripple-laminated, and/or bioturbated. A few thin lenses of mudstone/shale are present in the Chagray Formation. Marine bivalves (*Cardium levinae* Merklin, *Cyprina rotundata* Braun, *Lentidium* sp., and *Siliqua* sp.) and shark's teeth (Glikman, 1964) are present in the Chagray Formation at the Kumbulak Cliffs (Akhmetiev, 1994), whereas a terrestrial leaf flora is present at Altyn Chokysu (e.g., Zhilin, 1989; Andreyev, 1991).

ARAL FORMATION

The youngest Tertiary strata we studied belong to the Aral Formation, which has a maximum preserved thickness of 24.2 m in the Altyn Chokysu–Kumbulak Cliffs region. At Kintykche, on the western shore of the Aral Sea, about 240 km southwest of the Kumbulak Cliffs, a complete section of the Aral Formation is 27.5 m thick, where it is disconformably overlain by the Miocene (Burdigalian) Kintykche Formation (Akhmetiev, 1994). This suggests that most of the local thickness of the Aral Formation is preserved in the study area (Fig. 3).

The Aral Formation conformably overlies the Chagray Formation (Fig. 5, 6, 7A, 8A). Their contact is picked at the base of the lowest grayish yellow-green shale/claystone of Aral lithology above the highest Chagray sandstone. Typically, this lowest Aral Formation stratum and strata immediately above it contain abundant white shells of the bivalve *Corbula* (Fig. 8D), which weather over the slopes the Aral Formation forms above a cliff or bench defended by the Chagray Formation.

Most of the Aral Formation is grayish yellow-green calcareous shale and claystone (Fig. 5, 6, 7A, 8B). Less common lithologies are white to very pale orange calcarenite and limestone (Fig. 8C). Extensive, mammal-dominated fossil assemblages are known from the Aral Formation and are discussed below.
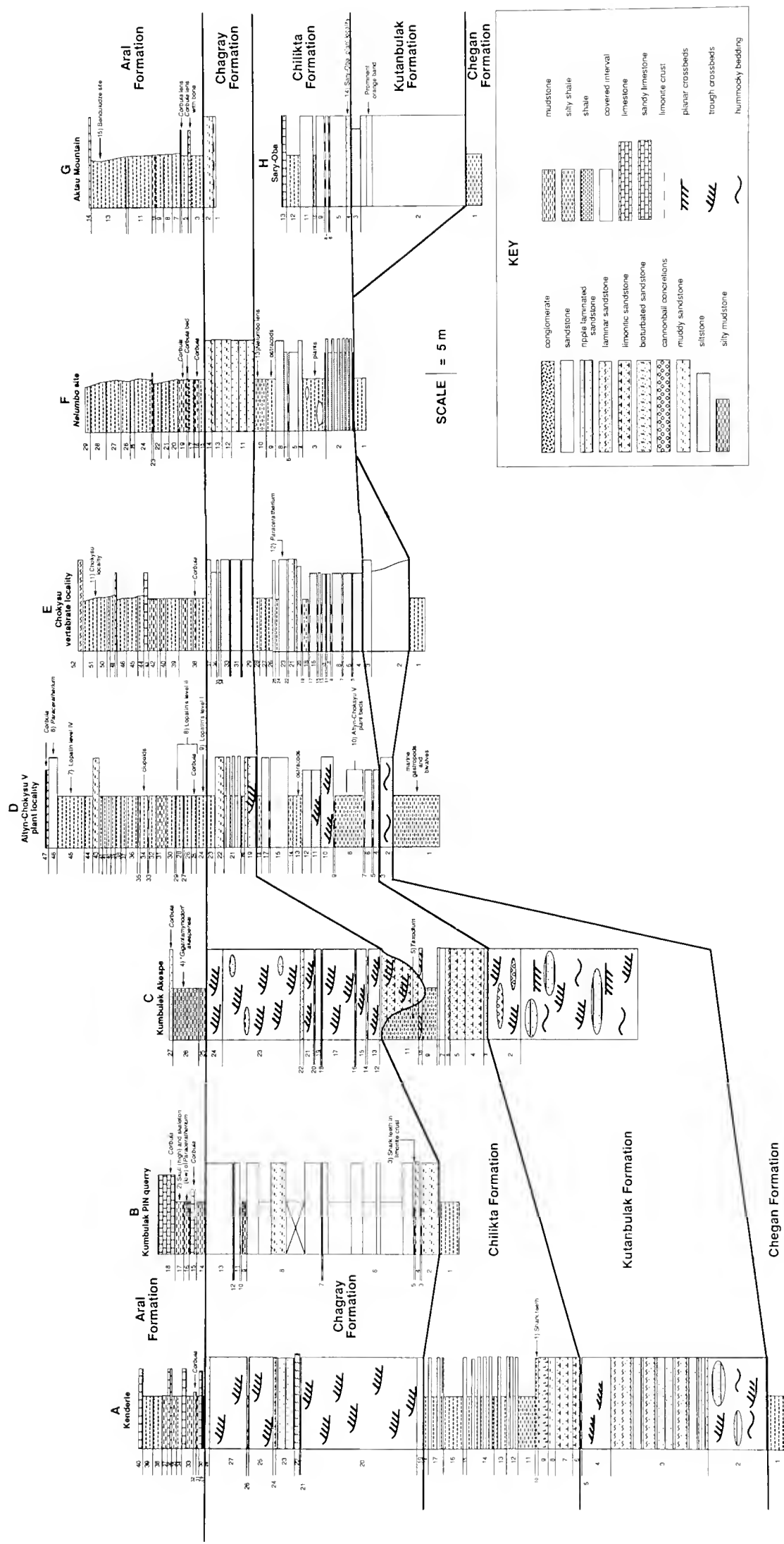
Fig. 5.—Measured stratigraphic sections of Oligocene strata in the Kumbulak Cliffs (sections A–C), Altyn Chokysu (sections D–F, H), and at Aktau Mountain (section G) showing fossil localities. See Appendix for description of numbered lithologic units in sections, and Table 1 for list of fossil localities.
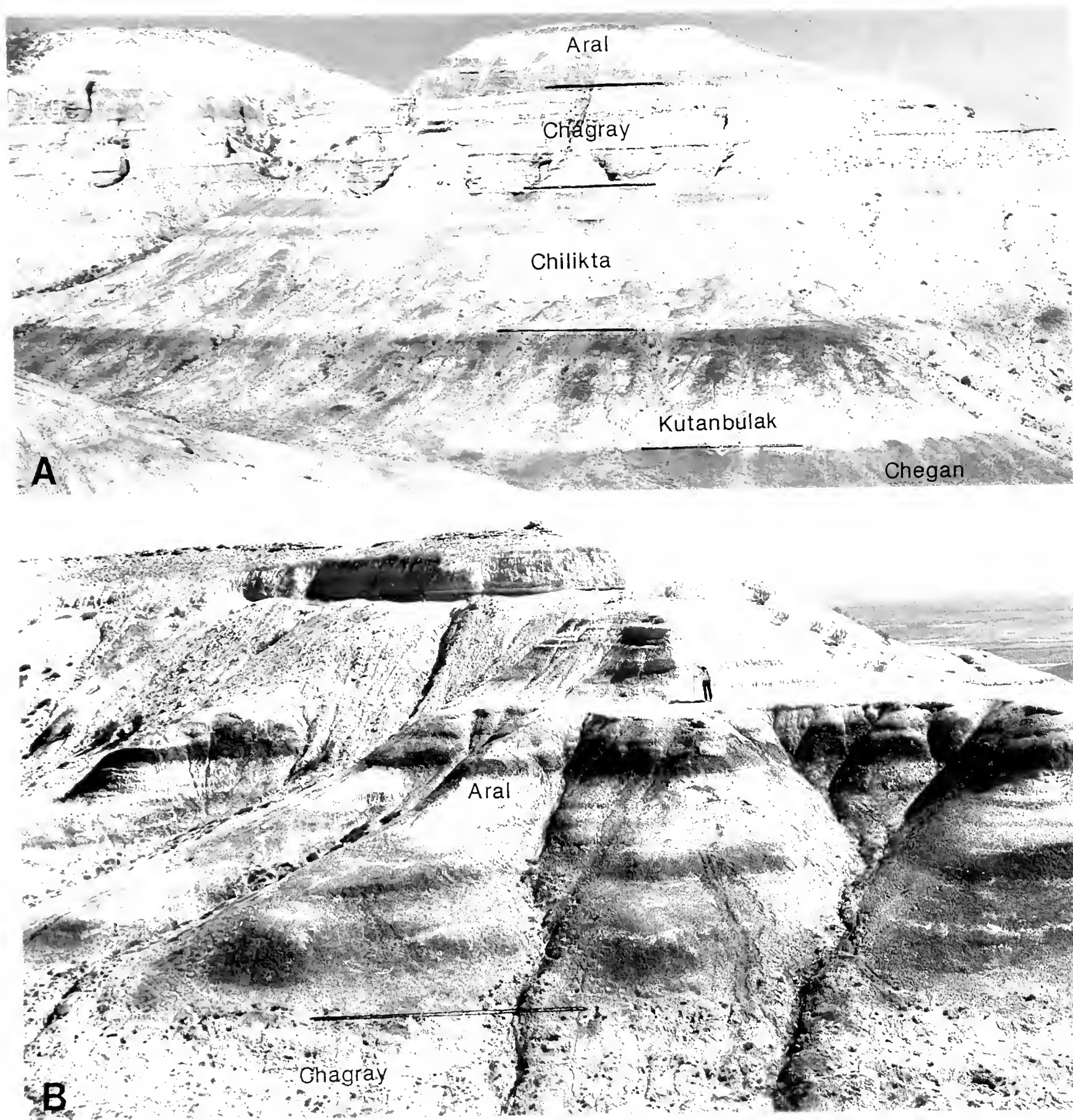
Fig. 6.—Selected outcrops of Oligocene strata at Altyn Chokysu. A. Overview of section E. B. Upper part of section D.

SEQUENCE STRATIGRAPHY

INTRODUCTION

Deposition of the Oligocene strata exposed in the Northern Priaral took place along the northeastern margin of the Paratethyan marine basin (e.g., Voznesenskiy, 1978; Marinescu, 1992). Lithology, facies architecture, and fossils indicate deposition took place in fully marine (Chegan), marginal ma-

rine (Kutanbulak, Chagray), and mixed marine/freshwater environments (Chilikta, Aral) (Yanshin, 1953; Voznesenskiy, 1978). Maximum thickness of the section is 164 m for rocks that supposedly span much of Oligocene time, about nine million years. Cumulative average sedimentation rates thus can be estimated as less than 2 mm/thousand years, which
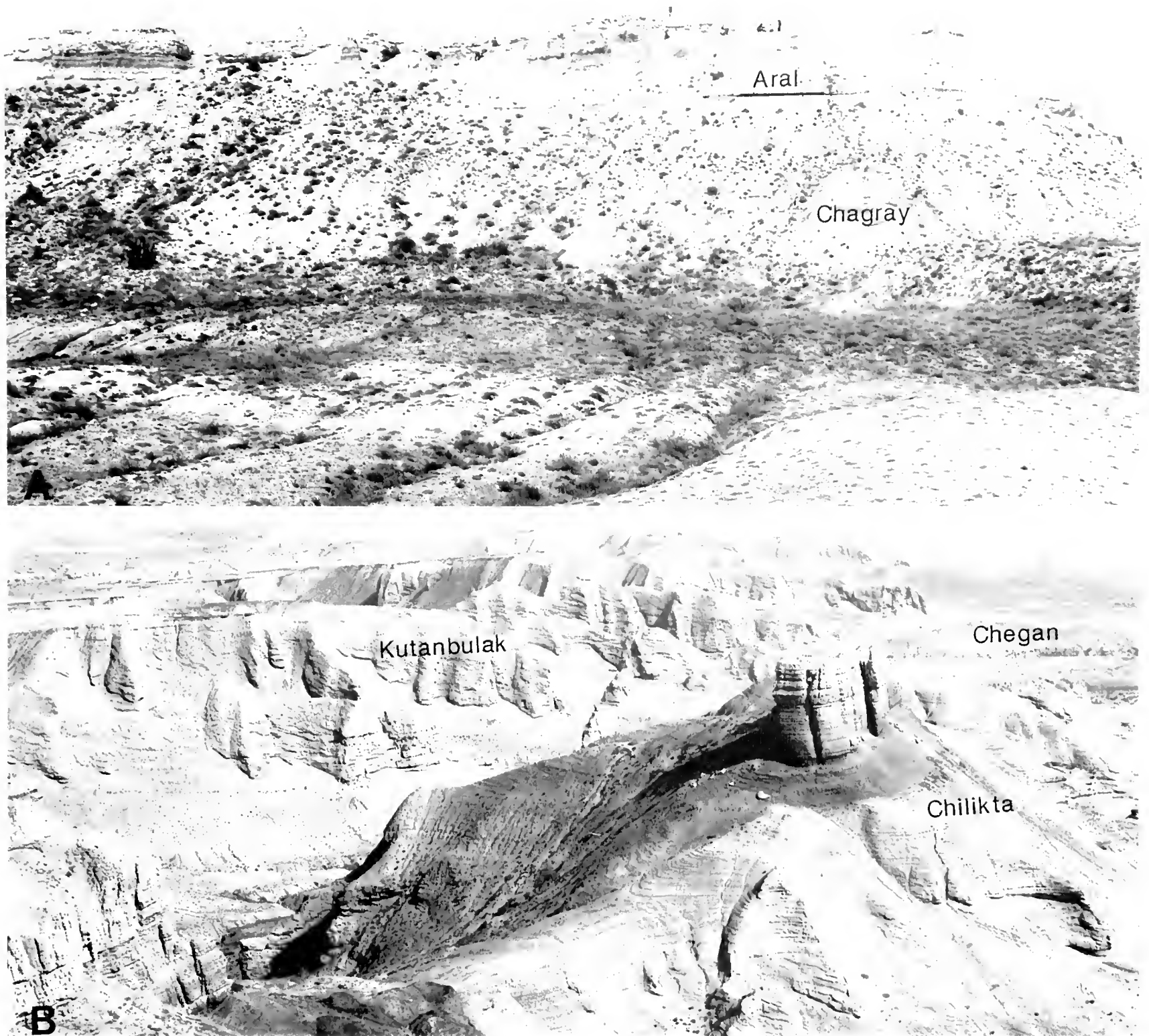
Fig. 7.—Overview of Oligocene strata at Kumbulak Cliffs. A. Upper part of section C. People are standing at locality 4. B. View of strata to east of section B.

is very low (Schindel, 1980; Sadler, 1981). No conglomerates are present in this section, and sandstones are very fine to fine grained and texturally and mineralogically submature to mature. Low thickness and low cumulative sedimentation rates, fine grain size, and maturity point to deposition under local conditions of tectonic quiescence.

Akhmetiev (1994) concluded that paleobotanical evidence indicates a subtropical climate during Kutanbulak deposition, followed by a warm temperate climate during Chilikta–Chagray deposition. Palynomorphs suggest a more arid climate during Aral deposition. However, these supposed climate changes may reflect little more than local facies

preservation, not regional or global climatic change that drove the depositional system. Tectonic quiescence and the lack of clear climatic cyclicity allow changes in relative sea level to be invoked as a factor that drove the Oligocene depositional system in the Northern Priaral (Voznesenskiy, 1978; Akhmetiev, 1994; Pinous et al., 1995).

The Oligocene outcrops exposed in the northern Priaral represent only a small part of a large depositional system that extended westward to Ustyurt, at least 700 km southwest of the area we studied. Therefore, sequence stratigraphic interpretation of our data must be considered preliminary, although it appears to be consistent with much of the regional
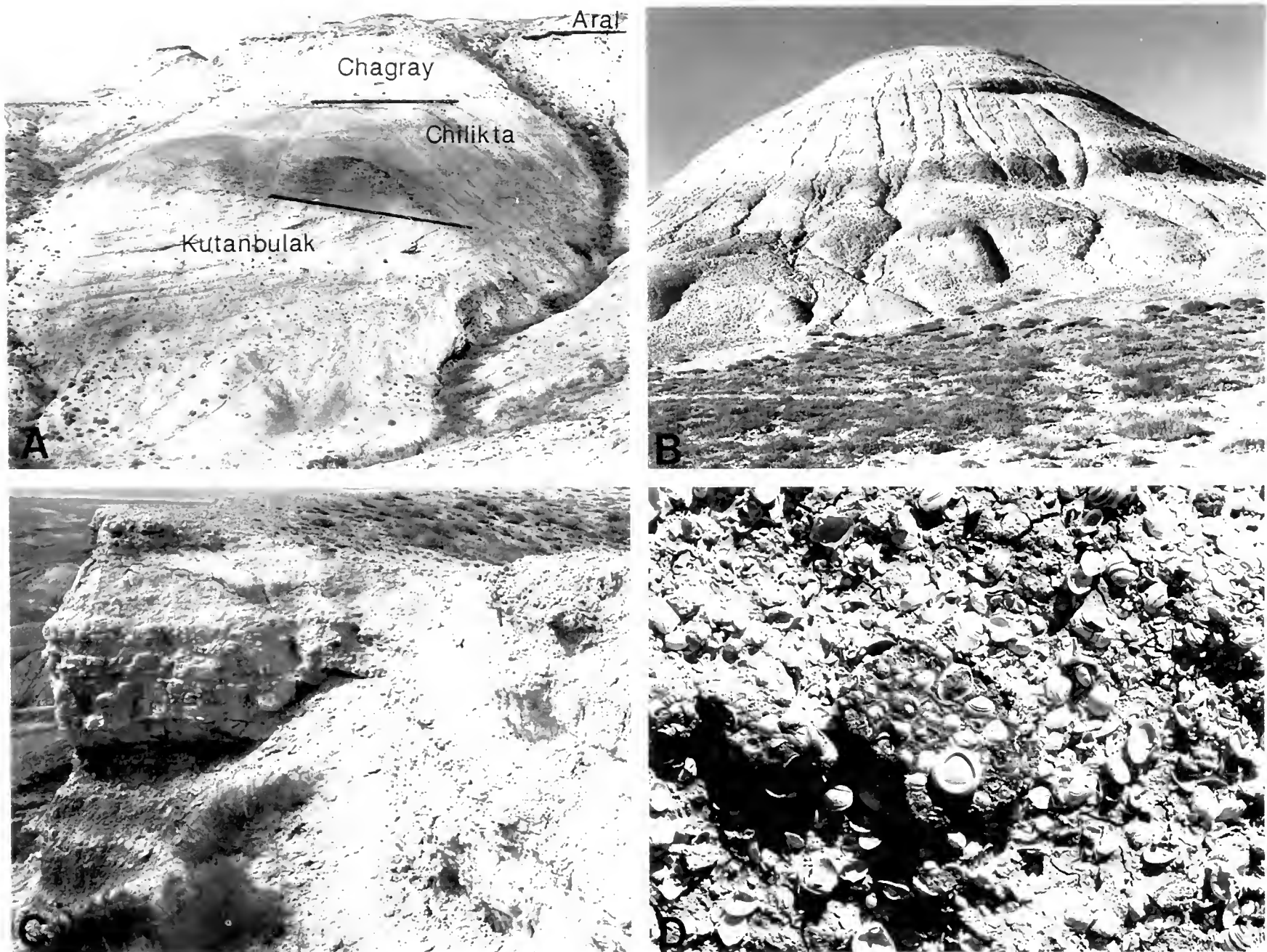
Fig. 8.—Selected outcrops of Oligocene strata in the study area. A. Outcrops west of section C showing Chilikta strata crosscutting Kutanbulak delta forests. B. Aral Formation strata at Aktau Mountain. C. *Paraceratherium* quarry (locality 2) in lower part of Aral Formation at Kumbulak Cliffs. D. *Corbula* coquina in Aral Formation at Aktau Mountain (Fig. 3:section G, unit 5).

stratigraphic framework for this depositional system developed by Voznesenskiy (1978).

Sequence stratigraphic interpretation of the Oligocene strata exposed in the Northern Priaral is important for correlation. It aids in interpreting the temporal relationships of relatively well-dated marginal marine units (Kutanbulak and Chagray) to overlying units dominated by freshwater deposits (Chilikta and Aral). It thus provides an indirect method of establishing the age of the fossil mammals from the Aral Formation, the central goal of this article.

UNCONFORMITIES

Our stratigraphic data (Fig. 5) identify two unconformities in the Oligocene strata of the Northern Priaral: one at the base of the Kutanbulak Formation, the other at the base of the Chagray Formation.

The unconformity at the base of the Kutanbulak

(Fig. 5) is marked by a dramatic lithologic change from Chegan bentonitic shale to Kutanbulak limonitic sandstone. Besides this pronounced grain size and lithologic change, this contact is characterized by scour-and-fill as well as the widely ranging thickness of the overlying Kutanbulak Formation. Indeed, in some sections the Kutanbulak is absent, and the Chilikta Formation rests directly on the Chegan (Fig. 5:section F). Similar lithologic changes (shale to sandstone), scour-and-fill, and wide variation in Chagray Formation thickness are associated with the unconformity between the Chilikta and Chagray formations (Fig. 5). The amount of stratigraphic relief on the sub-Kutanbulak unconformity, based on thickness changes of the Kutanbulak itself, is about 28 m. There is a comparable amount of stratigraphic relief on the sub-Chagray unconformity (based on Chagray thickness variations) of about 26 m.

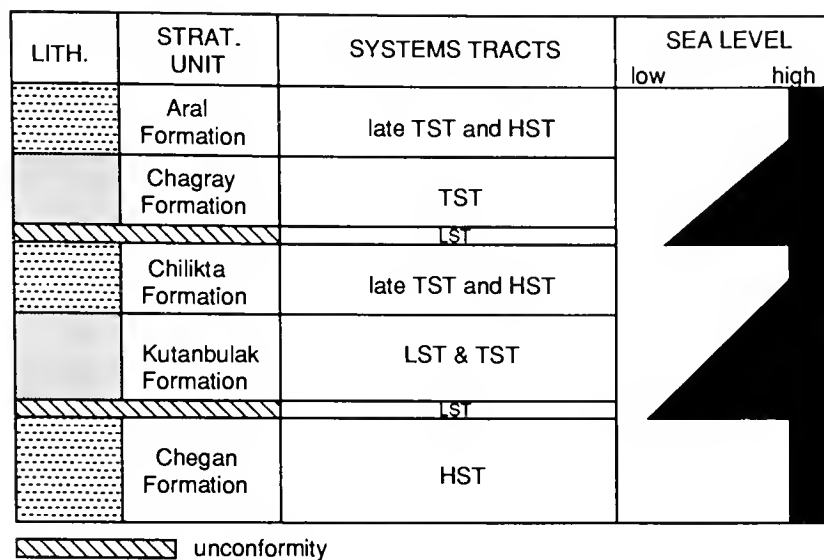| LITH.	STRAT. UNIT	SYSTEMS TRACTS	SEA LEVEL low high
	Aral Formation	late TST and HST	
	Chagray Formation	TST	
		LST	
	Chilikta Formation	late TST and HST	
	Kutanbulak Formation	LST & TST	
		LST	
	Chegan Formation	HST	

unconformity

Fig. 9.—Sequence stratigraphic interpretation of Oligocene strata in the study area.

Parts of two sequences and one complete sequence can thus be identified in the Paleogene strata of the study area (Fig. 9). These sequences are bounded by two unconformities—one at the base of the Kutanbulak Formation, the other at the base of the Chagray Formation.

Voznesenskiy (1978:fig. 3) and Akhmetiev (1994) identified the base of the Aral Formation as a regional unconformity. Our data do not support this. In the Northern Priaral, the base of the Aral Formation is a planar surface lacking scour-and-fill or other indicators of erosion. Chagray sandstones fine upward and become clayey just below the base of the Aral Formation, and lowermost Aral shales are sandy (e.g., Fig. 5:section A, Appendix). This suggests a transitional Chagray–Aral contact and supports our interpretation of the Chagray–Aral as representing one transgressive cycle of deposition (see below). Clearly, the Chagray–Aral contact is a paraconformity where Aral mudstone, shale, or silty shale rests on Chagray sandstone. However, it is not a major disconformity of geologically detectable temporal significance.

Significantly, Aral Formation thickness is relatively constant throughout the Northern Priaral. In contrast, the Baygubek Formation of the northern Ustyurt is about twice as thick as its homotaxial correlatives, the Aral and Chagray formations in the Northern Priaral (Fig. 3). These regional thickness changes are best explained as due to a sub-Chagray unconformity, well documented by our data (Fig. 5) and accepted by Voznesenskiy (1978) and Akhmetiev (1994), not by a sub-Aral unconformity.

MARINE INFLUENCE ON DEPOSITION

Based on fossil content, the strata described here range from open marine clastic shelf (Chegan) to marginal marine (Kutanbulak, Chagray) to mixed marine and freshwater (Chilikta, Aral). Vertebrate fossils provide direct evidence of marine influence in the Chilikta and Aral formations. Our locality 12 in the upper Chilikta Formation (Fig. 5:section E) produces tooth fragments of *Paraceratherium* (Lucas and Emry, 1996a) as well as an incomplete sirenian rib fragment and selachian teeth. The sirenian rib fragment, USNM (National Museum of Natural History, Smithsonian Institution, Washington, D.C.) 482244 (Fig. 10G–I), is a proximal fragment of an anterior rib. It is pachyostotic and compares favorably with sirenian ribs illustrated by Domning and Gingerich (1994:fig. 8) and Domning et al. (1994:fig. 7). The selachian teeth, USNM 482242 (Fig. 10A–D), belong to the sand tiger shark *Carcharias* and other lamniform taxa (Glikman, 1964).

The Aral Formation produces some cetacean remains (Lopatin, 1994a), including a small delphinid cervical centrum. This centrum, USNM 482245 (Fig. 10E, F), found at Altyn Chokysu near our locality 8, has a width of 33.9 mm and a length of 12.6 mm. It closely resembles delphinid centra illustrated by Mchedlidze (1988:pl. 5) but cannot be more precisely identified than Delphinidae.

The relatively unstudied fish fauna of the Aral Formation includes freshwater taxa as well as one marine group—clupeids (herrings) (Khisarova, 1977; Sychevskaya and Gurov, 1994, 1995). A thin claystone bed full of herring impressions is present at Altyn Chokysu in unit 34 of section D (Fig. 5).

Abundant fossils of the bivalve *Corbula* occur in the Aral Formation (Fig. 8D). *Corbula* is a Cretaceous–Recent bivalve characteristic of shallow marine and brackish water environments (e.g., Davies, 1971). Its presence in the Aral Formation provides additional evidence of marine influence on Aral sedimentation.

These indicators of marine influence contradict the paleogeography of Aral deposition proposed by Voznesenskiy (1978) and repeated by Akhmetiev (1994). Voznesenskiy (1978:fig. 33) reconstructed Aral deposition in a landlocked lacustrine basin well to the east of a Paratethyan shoreline in Ustyurt. However, the paleontological evidence just reviewed indicates that the Aral depositional system must have been directly connected to marine waters to allow fossils of *Corbula*, sharks, herrings, and dolphins to be preserved in the Aral Formation. Instead of a land-locked lake basin, Aral Formation deposition took place in a coastal estuarine basin
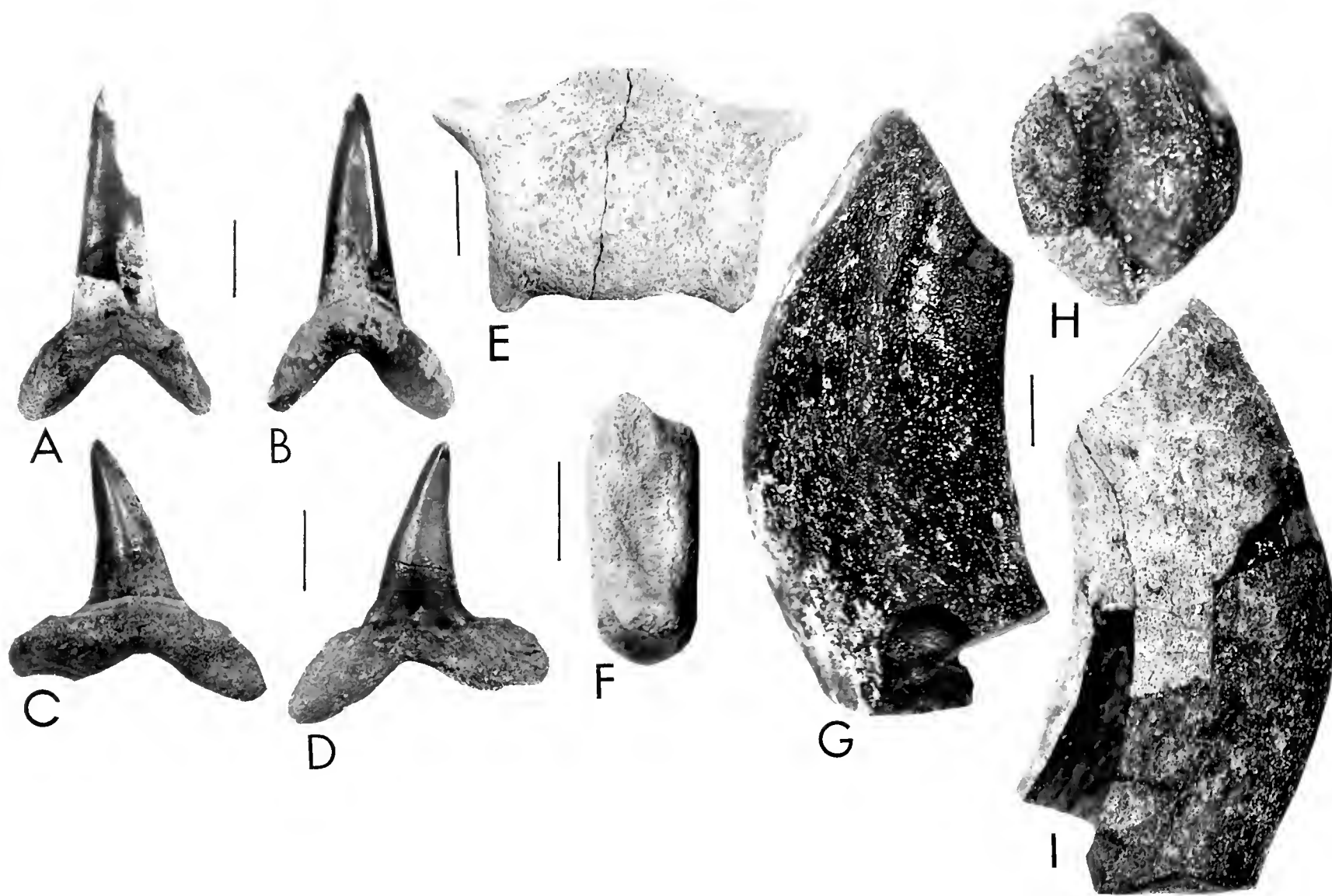
Fig. 10.—Selected vertebrate fossils indicative of direct marine influence on the deposition of the Chilikta and Aral formations. A–D. USNM 482242, lamniform shark teeth from the Chilikta Formation at locality 12. E, F. USNM 482245, Delphinidae, cervical vertebral centrum from the Aral Formation base near locality 8. G–I. USNM 482244, Sirenia, rib fragments, from the Chilikta Formation at locality 12. Scale bars = 1 cm.

that encompassed a mosaic of marine and fresh-water habitats.

Systems Tracts

We identify systems tracts in the Oligocene strata of the Northern Priaral (Fig. 9). In so doing, we employ the terminology and concepts of Posamentier and Vail (1988) and Posamentier et al. (1988). However, we follow Thorne and Swift (1991), who argue that fluvial strata that overlie an unconformity most likely represent a transgressive system tract (TST), not a lowstand systems tract (LST), as argued by Posamentier and his co-authors. We thus explain the facies architecture and unconformities in this section as follows (Fig. 9):

1. Chegan strata represent a highstand systems tract (HST) during which shales were deposited by relatively deep, well-circulated marine waters on a shelf below effective wave base. It is not clear whether the top of the Chegan Formation is every-where of early Oligocene age; locally, its top may be late Eocene (Akhmetiev, 1994). However, its youngest age establishes an early Oligocene age as the maximum age of the sub-Kutanbulak unconformity.

2. The sub-Kutanbulak unconformity records a base-level (sea- level) fall that exposed the Chegan shelf subaerially (type 1 unconformity). The exposed shelf underwent lowstand (LST) erosion and incision to produce an irregular landscape. Kutanbulak delta foresets downlap onto the sub-Kutanbulak unconformity basinward at the Kumbulak Cliffs (Fig. 7B). Landward, at Altyn Chokysu, the base of the Kutanbulak onlaps underlying Chegan shales (Fig. 6A).

3. Most Kutanbulak deposition was a response to rising base-level (TST) that caused aggradation of sand (Akhmetiev and Lucas, 1994). The irregular thickness of the Kutanbulak reflects the nature of the incised landscape upon which it was deposited. Delta foresets of the Kutanbulak at the Kumbulak Cliffs can be interpreted to represent a lowstand wedge deposited on the incised shelf. Thus, down-lapping Kutanbulak strata basinward (at the Kum-

Table 2.—*Mammalian fauna from the Aral Formation north of the Aral Sea. Compiled from Russell and Zhai (1987), Bendukidze (1993), and Lopatin (1994a, 1995). Localities are Alt-Ch = Altyn Chokysu, Ag = Agyspe (Kumbulak Cliffs), Ak = Aktau.*

Taxa	Alt-Ch	Ak	Ag
Erinaceidae			
Lanthanotherium sp.	×	×	
Amphechinus cf. *A. rectus*	×		
Amphechinus minimus	×		×
Amphechinus cf. *A. minimus*	×		
Palaeoscaptor acridens			×
Talpidae			
Mygalea lavrovi	×		
Asthenoscaptor sp.		×	
Proscapanus sp.	×		
Soricidae			
Gobisorex kingae	×		
G. aff. *G. kingae*	×	×	
"Palaeolagidae"			
Desmatolagus aff. *A. robustus*	×		
Desmatolagus aff. *D. schargaltensis*	×	×	×
D. simplex	×		×
Ochotonidae			
Sinolagomys aff. *S. kansuensis*	×	×	
Aplodontidae			
Plesispermophilus sp.	×		
Dipodidae			
Parasminthus aff. *P. tangingoli*	×		
Cricetidae			
Eucricetodon aff. *E. caducus*	×	×	×
E. aff. *E. asiaticus*			×
E. sajakensis	×	×	
E. aff. *E. youngi*	×		
Eumysodon orlovi			×
E. spurius	×		×
Argyromys aralensis			×
A. woodi			×
Protolactaga borissiaki			×
Eumyarion sp.	×		
Ctenodactylidae			
Yindirtemys sajakensis	×	×	
Y. birgeri	×	×	
Rhizomyidae			
Tachyoryctoides aff. *T. obrutschewi*	×	×	×
T. glikmani	×		
T. gigas	×	×	×
T. sp.	×	×	
Castoridae			
Steneofiber kumbulakensis	×		×
S. sp.			×
Agnotocastor sp.	×		×
Capatanka schokensis	×	×	×
Capacikala aff. *C. sajakensis*	×	×	
C. cf. *C. sciuroides*	×	×	
Asiacastor aff. *A. orientalis*	×	×	

Table 2.—*Continued.*

Taxa	Alt-Ch	Ak	Ag
Mustelidae			
new genus	×		
Perissodactyla			
Aprotodon borissiaki			×
Aceratherium aralense			×
Protaceratherium sp.			×
Paraceratherium prohorovi			×
Eggysodon sp.			×
Artiodactyla			
Lophiomeryx sp.			×
Prodremotherium sp.			×
Miomeryx sp.	×		×
Amphitragulus sp.	×		×
Micromeryx sp.			×
Cetacea			
Delphinidae	×		

bulak Cliffs) represent a lowstand wedge (LST), whereas onlapping Kutanbulak strata landward (Altyn Chokysu) are incised valley fills of an early TST (Fig. 9).

4. Continued rising base level produced lower Chilikta sandstones and interbedded shales (late TST). Peak base level led to ponding during late Chilikta deposition (HST). Laminated shales contain fossils of freshwater plants, including the water lily *Nelumbo* in growth position (Snigirevskaya and Zhilin, 1974). Fluvial deposition and deposition by Gilbert deltas that fed Chilikta lakes were controlled by local differential subsidence (autocyclic) or climate (allocyclic) factors.

The base of the Chilikta Formation locally downlaps Kutanbulak foresets basinward at the Kumbulak Cliffs (Fig. 8A). However, at most localities basinward, and at all localities landward (Altyn Chokysu), the base of the Chilikta onlaps the Kutanbulak or the Chegan (Fig. 5, 6A, 7B). Based on the local downlap, it could be argued that the top of the TST is the base of the Chilikta. However, the lower Chilikta (e.g., Fig. 5:section A, units 6–11) is a retrogradational parasequence set with a marine flooding surface (unit 10) near its middle. One or two more parasequence sets are preserved above the basal set (e.g., Fig. 5:section A, units 12–15 and 16–18) that appear to be aggradational parasequence sets that thin upward. This facies architecture suggests that the lower Chilikta represents the late TST, followed by HST, with uppermost progradational parasequence sets missing at the sub-Chagray unconformity.

5. Another fall in base level (sea level) produced the sub-Chagray unconformity, during which another incised landscape formed (on top of the Chilikta Formation) during lowstand ravinement (LST). The Chagray base onlaps the Chilikta throughout the Northern Priaral. We believe this is because the sub-Chagray unconformity (a type 1 unconformity) in the Northern Priaral is landward of the downlap surface, which Voznesenskiy's (1978:fig. 46) analysis suggests was in the Northern Ustyurt, well southwest of the Northern Priaral.

6. Chagray deposition took place during rising base level (early TST), which infilled the incised topography with sand. Retrogradational parasequence sets of the Chagray consist of thick, trough-crossbedded sandstones overlain by thin sandstones or sandy limestones with marine bivalves and shark's teeth (e.g., Fig. 5:section B, units 2–5).

7. Rising-to-peak base level produced an extensive complex of coastal estuaries and ponds during Aral time (late TST to HST). The lower part of the Aral Formation is made up of retrogradational parasequence sets in which relatively thick nonmarine mudstones are intercalated with thin *Corbula* packstones that represent marine flooding surfaces (e.g., Fig. 5:sec. F, units 15–19). The maximum flooding surface during Aral deposition may be the bed of clupeids, unit 34 of section D (Fig. 5). Above that, Aral strata are two aggradational parasequence sets, each composed of relatively thick nonmarine mudstone overlain by thin sandstone (Fig. 5:section D, units 35–43 and units 44–46). The *Corbula* bed at the top of section D (unit 47) may be the locally preserved base of a progradational parasequence set near the top of the HST.

Another sea-level fall separates the Aral from the overlying TST of the Kintykche Formation, not preserved in the study area. The Kintykche Formation produces gomphotheres (Akhmetiev, 1994), indicating it is of Miocene (probably Burdigalian) age.

CORRELATION

Recognition of three cycles of deposition driven by sea-level changes in the Paleogene of the Northern Priaral is an important aid to their global correlation. Particularly important is inclusion of the Aral Formation in the same sequence as the Chagray Formation. No significant unconformity separates the two units, which implies that the Aral Formation is not significantly younger than the underlying Chattian Chagray Formation.

Nevertheless, correlation of the sequence boundaries in the Oligocene strata of the Northern Priaral to the Exxon cycle curve for the North Atlantic basin (Haq et al., 1988) is not straightforward. The Exxon curve identifies five cycles of deposition during the Oligocene, two of Rupelian age and three of Chattian age. Only two Oligocene cycles of deposition are present in the Northern Priaral. These Priaral cycles can only be dated as Rupelian and Chattian, respectively, and cannot be more precisely correlated below the level of stage. Our stratigraphic data and the regional framework of Voznesenskiy (1978) suggest the maximum fall of sea level coincides to the sub-Chagray unconformity (Akhmetiev and Lucas, 1994), and this correlates well with the maximum fall in the Exxon curve, which is at the Rupelian–Chattian boundary.

The most straightforward interpretation is that the Oligocene strata of the Northern Priaral only record two of the five cycles of deposition recorded in the North Atlantic basin. Rather than being a relatively complete record of Oligocene time, the Northern Priaral strata only preserve fragments of the Rupelian and of the Chattian. We find this conclusion compelling because it also explains the extremely low average sedimentation rate of <2 mm/thousand years calculated above for the Northern Priaral section if it represents all of Oligocene time. This rate is well below any calculated average rate for fluvial, deltaic, or estuarine sedimentation (e.g., Schindel, 1980:fig. 1). Arguably, Oligocene sedimentation rates in the Northern Priaral were higher than 2 mm/thousand years, which they would be if the Oligocene strata in the Northern Priaral only represent relatively short intervals of the Oligocene.

FOSSIL LOCALITIES

We identified nine specific fossil mammal localities, five plant localities, and two shark's tooth localities of Oligocene age in the Altyn Chokysu–Kumbulak region (Fig. 2, 5; Table 1). One of the fossil mammal localities (12) is in the Chilikta Formation, and the rest are in the Aral Formation. Aral Formation fossil mammals along the Kumbulak Cliffs are mostly perissodactyls described by Borisyak (1939, 1944), Belyayeva (1954), Gromova (1959), and Bayshashov (1993) and artiodactyls listed (but not described) by Orlov (1939), Musakulova (1971), and Abdrakhmanova (1973). Argyropulo

(1939a, 1939b, 1940), Shevyreva (1967), Lychyov (1970), and Bendukidze (1993) described the rodents from these localities. Bendukidze (1993) and Lopatin (1994a, 1994b, 1995) described the small-mammal-dominated assemblages from the Aral Formation at Altyn Chokysu and Aktau Mountain.

Fossil mammal localities in the Aral Formation at the Kumbulak Cliffs are from the lower 5 m of the formation (Fig. 5). Correlative mammal localities are present in the Aral Formation at Altyn Chokysu (Fig. 5). However, also at Altyn Chokysu, and at Aktau Mountain, mammals occur much higher stratigraphically in the Aral Formation, as much as 23 m above its base (Fig. 5). Lopatin (1994a, 1994b) claimed there are differences in the composition of the mammalian fossil assemblages from low and high in the Aral Formation at Altyn Chokysu. However, his data and those of Bendukidze (1993) do not support this. They indicate essentially identical micromammal assemblages occur low and high in the Aral Formation at Altyn Chokysu. Therefore, we treat all fossil mammal assemblages from the Aral Formation as part of a single fossil assemblage we term the Aral local fauna. The Aral local fauna thus consists of a diverse array of micro- and megamammals (Table 2; Fig. 11).

MAMMALIAN BIOCHRONOLOGY

MICROMAMMALS

Micromammal assemblages of the Aral local fauna consist of insectivores, lagomorphs, and rodents (Table 2). Bendukidze (1993) provided the most extensive documentation of these fossils; Lopatin's (1994a, 1994b, 1995) preliminary reports await more complete publication.

Most Aral Formation erinaceids suggest an Oligocene age. *Amphechinus minimus* is a typical Tabenbulukian taxon originally described by Bohlin (1946) from Yindirte in Gansu, China. *Amphechinus rectus* also is known from Yindirte, although Matthew and Granger (1924) originally described it from older, Shandgolian strata at Loh, Mongolia. In Europe, *Amphechinus* has a temporal range of late Oligocene–early Miocene (Brunet et al., 1981; De Bruijn et al., 1992). *Palaeoscaptor acridens* is a well-known Shandgolian–Tabenbulukian taxon in China–Mongolia (Russell and Zhai, 1987). The soricid *Gobisorex kingae* is a Shandgolian taxon (Sulimski, 1970).

Bendukidze (1993) reported the characteristically Miocene genus *Lanthanotherium* (De Bruijn et al., 1992; Qiu and Qiu, 1995) from Altyn Chokysu based on two M_1s. However, these relatively large teeth have trigonids that are longer than wide with three trenchant cusps and deep talonid basins with trenchant hypoconids and entoconids; they cannot be distinguished from M_1 of *Amphechinus* (see Matthew and Granger, 1924; Bohlin, 1942). Therefore, we reject Bendukidze's (1993) identification of *Lanthanotherium* in the Aral local fauna.

Bendukidze (1993) referred talpids from the Aral Formation to three genera—*Mygalea, Asthenoscaptor,* and *Proscapanus*—known from the European Miocene (Hutchison, 1974; Van den Hoek, 1989;

Ziegler, 1990). Talpids have a limited Paleogene fossil record, especially in Asia (Russell and Zhai, 1987), so we attach no biochronological significance to their record in the Aral local fauna.

Lagomorphs from the Aral Formation indicate an Oligocene age. *Desmatolagus robustus* Matthew and Granger, 1923, originally described from the Shandgolian of Mongolia, ranges in age from Ergilian to Shandgolian in Mongolia–China (de Muizon, 1977).

Desmatolagus shargaltensis Bohlin, 1937 is known from the Tabenbulukian Shargaltein Gol assemblage in Gansu, China. *Desmatolagus gobiensis* Matthew and Granger, 1923 ranges in age from Ergilian to Shandgolian in China–Mongolia (Shuvalov and Reshetov, 1974; Sych, 1975; Wang et al., 1981). Indeed, Qiu and Qiu (1995) identify *Desmatolagus* as a characteristic Oligocene genus (also see Russell and Zhai, 1987).

The ochotonid *Sinolagomys gracilis* Bohlin, 1942 is known from the Tabenbulukian at Shargaltein Gol in Gansu. Like the other Aral lagomorphs, it suggests a late Oligocene age. Indeed, none of the taxa of Aral lagomorphs is known from Miocene strata except the genus *Sinolagomys*, which has its last occurrence (*S. pachygnathus*) in the early Shanwangian of China (Qiu and Qiu, 1995).

The Aral rodent assemblage is of Asian affinities. Only *Eucricetodon* is also found in Europe, where it ranges in age from Oligocene to as young as MN3, which is very earliest Miocene (De Bruijn et al., 1992). In an abstract, Lopatin (1995) reports a new species of *Eumyarion* from the Aral Formation at Altyn Chokysu. He states that this species is similar to *E. carbonicus* but more primitive dentally with a reduced posterior arm of the hypoconid on
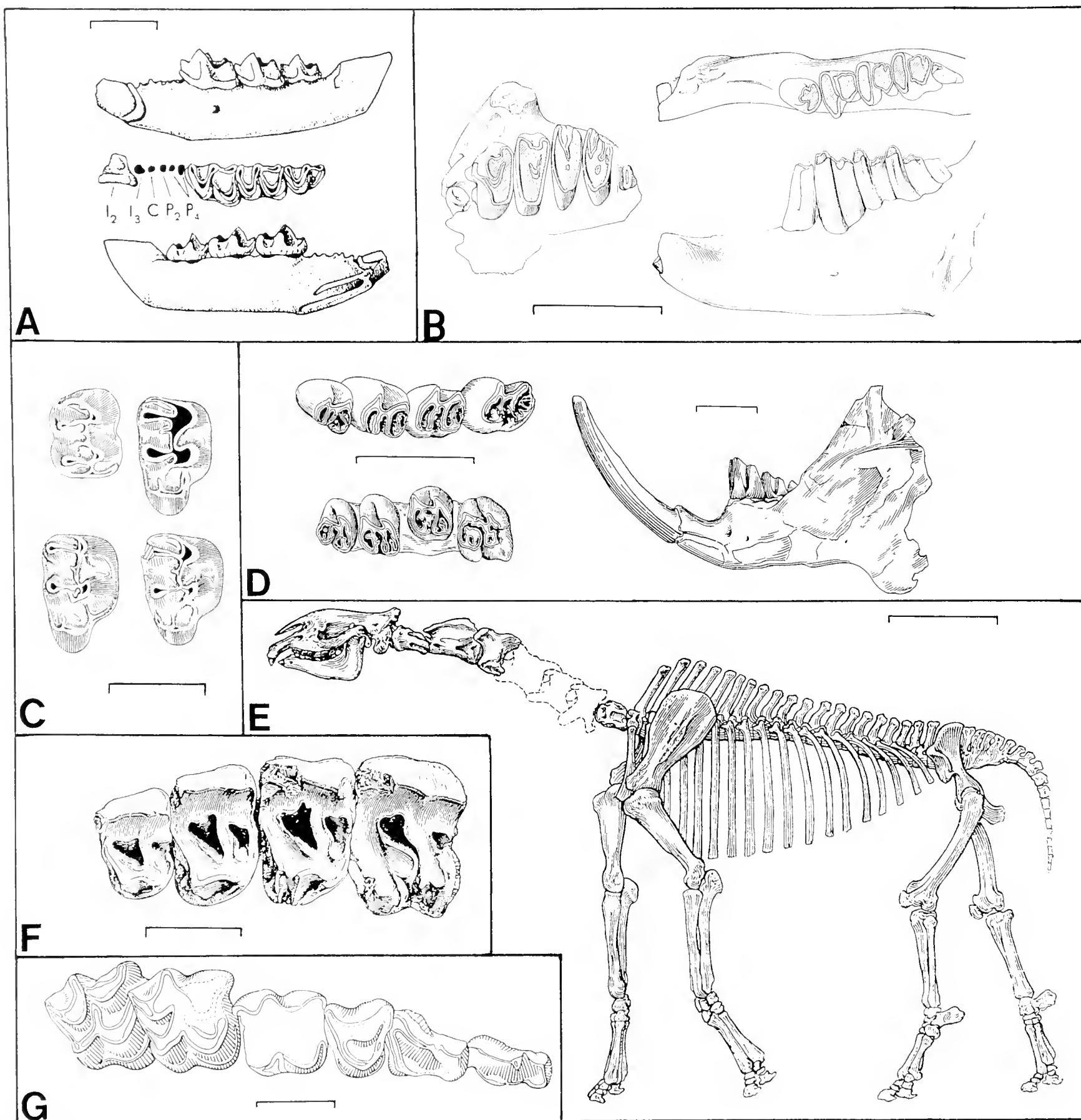
Fig. 11.—Selected fossil mammals representative of the Aral local fauna. A. *Gobisorex kingae*, left dentary with I$_2$, M$_{1-3}$, labial (above), occlusal (middle), and lingual (bottom) views; after Sulimski (1970); scale bar = 2 mm. B. *Desmatolagus robustus*, occlusal view of left P^3–M^2 (left), and occlusal (top right) and labial (bottom right) views of left dentary with P$_4$–M$_3$; after Matthew and Granger (1923); scale bar = 10 mm. C. *Eucricetodon*, occlusal views of right M$_2$ (top left) and left M^{1}s; after Fejfar (1987); scale bar = 20 mm. D. *Propalaeocastor kumbulakensis*, occlusal views of left P$_4$–M$_3$ (top left) and left P^4–M^3 (bottom left), and labial view of left dentary; after Lychyov (1970); scale bars = 10 mm. E. *Paraceratherium*, skeleton; after Gromova (1959); scale bar = 1 m. F. *Aceratherium aralense*, occlusal view of left P^2–M^1; after Borisyak (1944); scale bar = 30 mm. G. *Lophiomeryx*, occlusal view of right P^2–M^3; after Brunet and Sudre (1987); scale bar = 10 mm.

its lower molars. *Eumyarion carbonicus* is of latest Oligocene age (MN1–2 correlative: Sümengen et al., 1990; De Bruijn and Saraç, 1991), so the *Eumyarion* reported by Lopatin supports a late Oligocene age for the Aral local fauna.

Plesispermophilus (assigned to the Aplodontidae as *Prosciurus* by Kowalski [1974] and Schmidt-Kittler and Vianey-Liaud [1979]) is known from the Shandgolian of Mongolia and Chelkar-Teniz in north-central Kazakstan (Matthew and Granger, 1923; Shevyreva, 1976). The dipodid *Parasminthus tangingoli* Bohlin, 1946 ranges in age from Shandgolian to Tabenbulukian in China–Mongolia (Kowalski, 1974; Wang et al., 1981; Huang, 1982). The genus *Parasminthus* has its youngest record in the Xiejia fauna of Qinghai, China (Li and Qiu, 1980).

Eucricetodon is known throughout Eurasia from strata that range in age from early Oligocene to early Miocene (Russell et al., 1982; Russell and Zhai, 1987; De Bruijn et al., 1992; Qiu and Qiu, 1995). *Eucricetodon caducus* occurs at Kyzylkak in central Kazakstan in Shandgolian strata (Russell and Zhai, 1987). *Eucricetodon asiaticus* also occurs there, and in Shandgolian strata in Mongolia (Kowalski, 1974). *Eucricetodon sajakensis* is endemic to the Aral local fauna, and *E. youngi* was described from the Xiejia local fauna in Qinghai, China (Li and Qiu, 1980), the type fauna of the Xiejiaan land mammal age, a possible correlative of MN2 (Qiu and Qiu, 1995). *Eumysodon orlovi* and *E. spurius* are endemic to the Aral local fauna, as are *Argyromys aralensis*, *A. woodi*, and *Protolactaga borissiaki*.

Bohlin (1946) named *Yindirtemys woodi* from the type Tabenbulukian mammal assemblage at Yindirte in Gansu, China. Bendukidze's (1993) species *Y. sajakensis* and *Y. birgeri* are endemic to the Aral local fauna.

Steneofiber kumbulakensis also is endemic to the Aral local fauna. The genus *Steneofiber* is of Oligocene and Miocene age (Russell and Zhai, 1987). *Agnotocastor* has been reported from Shandgolian? strata at Myneske–Suyek in the Turgay region of north-central Kazakstan (Lychyov, 1978; Badamgarov and Reshetov, 1985; Russell and Zhai, 1987).

Capatanka and *Capacikala* are unknown in Eurasia outside of the Aral local fauna. Macdonald (1963) named these flat-incisored castorids from the Sharps Formation of South Dakota (USA), and they are also known from the Harrison Formation of Nebraska (Tedford et al., 1987). These are records of well-established early Arikareean age, late Oligocene (Sharps Formation), and earliest Miocene

(Harrison Formation) (Tedford et al., 1987). Bendukidze (1993:pls. 26, 27) based his identifications of these castorids solely on cheek teeth that do not strike us as particularly similar to those of either *Capatanka* or *Capacikala*. These identifications of North American taxa thus need to be reevaluated.

Lychyov (1982, 1987; Lychyov and Aubekerova, 1971) described *Asiacastor* from localities in the Semipalatinsk and Zaysan regions of eastern Kazakstan. He assigned these occurrences a Miocene age, although there is no clear basis for the age assignment. Therefore, there is no reason to use *Asiacastor* to assign a Miocene age to the Aral local fauna.

MEGAMAMMALS

Aral Formation Carnivora (an undescribed mustelid) and Cetacea (an indeterminate delphinid) are of no biochronological significance. In contrast, Aral Formation perissodactyls are relatively well documented. None of the Aral Formation perissodactyls are known from the European Neogene (De Bruijn et al., 1992), nor are any known from the Chinese Neogene (Qiu and Qiu, 1995). They thus provide strong evidence of an Oligocene age. We note here, however, that the supposed Aral Formation amynodontid, *Gigantamynodon akespensis* Bayshashov, 1993, is actually based on a specimen of rhinocerotid, probably *Protaceratherium* (Lucas and Emry, 1996b).

Two undocumented taxa reported by Bendukidze and listed by Russell and Zhai (1987) are *Eggysodon* sp. and *Protaceratherium* sp. Records of *Eggysodon* in central Kazakstan, the Georgian Republic, Mongolia, and China are considered to be of late Oligocene age (Belyayeva, 1954; Gabuniya, 1964, 1981; Brunet, 1979; Reshetov et al., 1993). Some authors consider *Protaceratherium* to be a synonym of *Aceratherium* (but see Heissig, 1989). In Europe, *Aceratherium* sensu lato ranges in age from MP 23 to MP 28, late Oligocene (Russell et al., 1982; Brunet and Vianey-Liaud, 1987). The genus *Aceratherium* has also been reported in China from the Shandgolian (Huang, 1982). *Aceratherium aralense* is known from Myneskesuyek, Kyzylkak, and some other Oligocene localities in central Kazakstan (Kordikova, 1994).

Aprotodon borissiaki is also known from the Tabenbulukian of Askazansor in the Betpak Dala desert of central Kazakstan (Belyayeva, 1954; Russell and Zhai, 1987). The genus has been reported from the Shandgolian of Nei Mongol, China (Wang et al., 1981).

Paraceratherium (= *Indricotherium*, = *Dzungariotherium*, = *Baluchitherium*: Lucas and Sobus, 1989; although Spassov [1989] and Kordikova [1990, 1995] suggest *Indricotherium* is a distinct genus) occurs in late Oligocene deposits in eastern Europe (Petronijevic and Thenius, 1957; Gabuniya and Iliescu, 1960; Russell et al., 1982). In China–Mongolia, *Paraceratherium* ranges from the Shandgolian to Tabenbulukian. Its possibly youngest record there is in the Shawa Formation of the southern Junggar Basin, Xinjiang, where *Paraceratherium* co-occurs with *Lophiomeryx* (Qiu, 1965, 1973). (However, note that this may not be true *Lophiomeryx* according to Qiu and Qiu [1995].) Qiu and Qiu (1995) regard these two taxa as correlative to the Lanzhou fauna and assign them an early Miocene age correlative to MN1. If the MN1 correlation is correct, then the Shawa taxa are latest Oligocene. We prefer a more parsimonious age assignment of Tabenbulukian sensu Russell and Zhai (1987), not Xiejiaan, for the Shawa Formation mammals.

Apparently, the only bona fide Miocene occurrence of *Paraceratherium* is at Bugti in Pakistan (Lucas, 1994). The Bugti mammal assemblage shares very few taxa with the Aral assemblage—*Aceratherium*, *Paraceratherium*, and *Prodremotherium*? (Raza and Meyer, 1984). Bugti largely has endemic rodents (Flynn et al., 1986), diverse anthracotheres, and proboscideans unknown in the Aral. The Bugti mammal assemblage is correctly regarded as being of early Miocene age, a refugium for *Paraceratherium* and amynodontids (Raza and Meyer, 1984). It postdates the "proboscidean datum" (Tassy, 1990) and is younger than the Aral local fauna.

Five genera of artiodactyls have been identified from the Aral Formation (Table 2), but no specimens have been described or illustrated (Orlov, 1939; Musakulova, 1971; Abdrakhmanova, 1973). We have not been able to locate or examine any of the specimens upon which these identifications are based, so we regard their biochronological significance as tentative.

Russell and Zhai (1987:384) noted that *Prodremotherium*, *Amphitragulus*, and *Lophiomeryx* are present in the European late Oligocene, and used this to support a late Oligocene age for the Aral local fauna. *Prodremotherium* and *Lophiomeryx* are unknown from the European Neogene, but *Amphitragulus* occurs at horizons as young as MN5 (Vislobokova, 1992), which is late Burdigalian (De Bruijn et al., 1992).

The muntjac *Micromeryx* is not an Oligocene tax-

EPOCH	STAGE	EUROPE LMA	MAMMAL ZONES	CHINA LMA	NORTHERN PRIARAL
MIOCENE	BURDIGALIAN	ORLEANIAN	MN5	SHANWANGIAN	Kintykche Formation
			MN4		
			MN3		
	AQ	AGENIAN	MN 2b	XIEJIAAN	
			MN 2a		Aral Formation
			MN1		
OLIGOCENE	CHATTIAN	ARVERNIAN	MP 25–MP30	TABENBULUKIAN	
					Chagray Formation

Fig. 12.—Correlation of the Northern Priaral Oligocene strata to the European succesion of MP and MN zones (Fahlbusch, 1976; Russell et al., 1982; Schmidt-Kittler, 1987; Steininger et al., 1990) and to the Chinese land-mammal "ages" (lma) of Qiu and Qiu (1995).

on; it occurs in zones MN2–8, so it is wholly Miocene in Europe (Vislobokova, 1992). *Miomeryx*, however, is a late Eocene–Oligocene taxon known from the Ergilian–Shandgolian of China and Mon-

golia (Matthew and Granger, 1925; Mellett, 1968; Shuvalov and Reshetov, 1974; Wang and Zhang, 1983). Thus, other than *Micromeryx*, the Aral Formation artiodactyls suggest an Oligocene age.

LATE OLIGOCENE AGE OF THE ARAL LOCAL FAUNA

Most taxa of Aral Formation mammals are late Oligocene (Arvernian, Tabenbulukian) forms unknown from the Neogene of Europe or China–Mongolia. Only a few poorly documented taxa—talpids and the muntjac *Micromeryx*—are Miocene forms unknown elsewhere from the Oligocene. Therefore, based on the presence of many well-established late Oligocene taxa, and the virtual absence of well-established early Miocene taxa, we assign the Aral local fauna a late Oligocene age (Fig. 12). Other mammal localities in the Aral Formation to the southwest of the Northern Priaral (Sayaken, Kuzhasay, and Zhilansay) do not challenge this conclusion. These localities yield essentially the same taxa as are found in the Aral Formation in the Northern Priaral. Indeed, they add only one mammal taxon to the Aral Formation, *Tataromys*, a rodent well known from the Shandgolian–Tabenbulukian of China–Mongolia (Russell and Zhai, 1987).

Bendukidze (1977, 1993) and Lopatin (1994*a*, 1994*b*, 1995) both assign the Aral local fauna an early Miocene age (also see Gabuniya, 1981, 1986; Agadzhanyan, 1986; Akhmetiev et al., 1995). This is partly because they consider MN1, to which Lopatin (1994*a*, 1994*b*) explicitly correlates the Altyn Chokysu micromammal assemblages, to be of early Miocene age, which it is not (Steininger et al., 1990).

Both Bendukidze and Lopatin argue that Aral lagomorphs and rodents are more evolutionarily advanced (progressive) than the Tabenbulukian taxa to which they are assigned. For that reason, they argue the Aral micromammals are younger than Tabenbulukian. We prefer a more robust correlation based on the presence or absence of index taxa, not on evaluations of evolutionary grade. We wonder why, if the Aral micromammals are so progressive over their Tabenbulukian relatives, are they being assigned to Tabenbulukian taxa? Clearly, some taxonomic revision of the Aral micromammals is needed, but to produce a Miocene assemblage would require a total makeover of the micromammal fauna. In particular, well-grounded identifications of Oligocene index taxa such as *Desmatolagus* and *Yindirtemys* would have to be abandoned, or at least it would have to be argued that the Aral local fauna represents the only Miocene record of these taxa. Against this is a megamammal assemblage from the Aral Formation dominated by Oligocene taxa, particularly the perissodactyls. We thus conclude that, based on fossil mammals, there is no strong evidence that the Aral local fauna is Miocene, but compelling evidence that it is late Oligocene.

PALEOBOTANICAL CORRELATIONS

Paleobotanical correlation is the principal reason some Russian workers advocate an early Miocene age for the Aral Formation (Akhmetiev, 1994) or even for the underlying Chagray Formation (Andreyev, 1991; Zhilin and Andreyev, 1994). Andreyev (1991; Zhilin and Andreyev, 1994) divides the paleofloral localities at Altyn Chokysu into two stratigraphic (temporal) levels. Localities stated to be from the Chilikta Formation (Altyn Chokysu plant localities I, III, V, VII, and IX) are supposed to be Chattian, and those assigned to the Chagray Formation (Altyn Chokysu II, IV, and VI) are termed Aquitanian. According to Andreyev (1991) and Zhilin and Andreyev (1994), both horizons produce paleofloras of the "Turgay complex" that indicate a warm, temperate climate. Putative index taxa (e.g., Chattian *Apocynophyllum helveticum* and Aquitanian *Myrica longifolia*) establish the different ages of the two horizons.

Our stratigraphic data (Fig. 5) undermine the paleofloristic correlations advocated by Andreyev (1991) and Zhilin and Andreyev (1994; also see Zhilin, 1989). In particular, they identify the Sary Oba plant locality (Altyn Chokysu VI) as Aquitanian, but it is actually stratigraphically below their "Chattian" locality Altyn Chokysu V (*Nelumbo* lens). Indeed, Altyn Chokysu VI is not in the Chagray Formation as claimed by Andreyev (1991) and Zhilin and Andreyev (1994), but at the very base of the Chilikta Formation. Possibly an Aquitanian fossil plant locality being apparently lower stratigraphically than a Chattian fossil plant locality could be explained by time transgression of lithofacies. But, this seems unlikely over the 8 km that separate the two sites given the lateral continuity of lithofacies at Altyn Chokysu (Fig. 2, 5; Appendix).

Furthermore, there seems to be no clear paleobotanical basis for locating the Oligocene–Miocene boundary in sections of well-established age in Europe. Instead, floristic change across this boundary

has been described as prolonged, complex, and asynchronous (e.g., Kovar-Eder, 1994). This undermines our faith in the putative Chattian and Aquitanian index plant taxa identified by Akhmetiev, Andreyev, and Zhilin.

The Altyn Chokysu paleofloral localities represent a variety of taphofacies. For example, Altyn Chokysu V in silty/sandy shale preserves isolated leaves and foliar fragments, whereas Altyn Chokysu II, in a similiar lithology, yields complete water lilies in growth position. At Altyn Chokysu VI, leaves are preserved as oxidized impressions in sandstone concretions. These differences in taphonomy more

likely explain the differences in taxonomic composition between these localities than do differences in age. Paleobotanists need to analyze paleofloral succession in the Oligocene of the Northern Priaral while controlling for, and factoring out, the effects of different lithofacies and taphofacies. Until this is done, and until a paleofloral basis can be established for placement of the Oligocene–Miocene boundary in well-dated sections elsewhere, paleofloral correlations of the Oligocene strata in the Northern Priaral are unconvincing. Paleobotanical correlations thus do not provide a basis for assigning a Miocene age to the Aral Formation.

CONCLUSIONS

Mammalian biochronology indicates that the fossil mammals of the Aral Formation (Aral local fauna) are of late Oligocene age. Our sequence stratigraphic interpretation supports assigning a late Chattian age to the Aral Formation. Our lithostratigraphy undermines paleobotanical correlations that assign a Miocene age to the Aral Formation.

The Aral Formation mammals are of Tabenbulukian age, and provide an indirect but strong correlation of the Tabenbulukian to part of Chattian time. The Aral local fauna thus emerges as one of the best documented Tabenbulukian assemblages known from Asia.

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APPENDIX

Description of Measured Sections

A—Kenderle

Section begins at UTM 41319027E, 5184292N, on southwest tip of hill; top of section is at top of Kenderle Mountain, 41319512E, 5184430N. This is the type section of the Kutanbulak, Chilikta, and Chagray svitas.

Unit	Lithology	Thickness (m)

Aral Formation:

40 Limestone; white (N9) to light greenish gray (5GY8/1); micritic; forms a ledge. 0.6

39 Shale; pale olive (10Y6/2). 1.6

38 Shale; light greenish gray (5GY8/1). 1.5

37 Claystone; light greenish gray (5GY8/1); marly. 0.7

36 Limestone; same lithology as unit 33; forms a ledge. 0.6

35 Claystone; light greenish gray (5GY8/1); marly. 0.8

34 Shale; light greenish gray (5GY8/1); rhizoliths; very calcareous. 0.7

33 Shale; pale olive (10Y6/2); carbonate nodules; top 0.6 m forms a white limestone ledge like unit 32, but without *Corbula*. 1.6

32 Calcareous shale; white (N9) with *Corbula*; forms a ledge. 0.4

31 Shale; moderate orange pink (5YR8/4); very calcareous. 0.3

30 Clayey limestone; white (N9) to light greenish gray (5GY8/1); calcarenite of fine to very coarse limestone chips. 0.5

29 Sandy shale; pale olive (10Y6/2). 0.1

Chagray Formation:

28 Clayey sandstone; dark yellowish orange (10YR6/6) limonitic band. 0.9

27 Sandstone; same colors and lithology as unit 20; light greenish gray (5GY8/1) unweathered. 5.8

26   Muddy sandstone and sandy mudstone; yellowish gray (5Y8/1) and light greenish gray (5GY8/1); fine-grained, subangular quartzarenite; not calcareous.   0.3

25   Sandstone; same colors and lithology as unit 20.   3.8

24   Sandstone; pale greenish yellow (10Y8/2) and grayish yellow (5Y8/4); calcareous; very fine-grained quartzarenite; hummocky bedded; forms a thin bench.   0.4

23   Sandstone; same colors and lithology as unit 20; laminated.   2.9

22   Limonitic sandstone; dark yellowish orange (10YR6/6) and moderate yellowish brown (10YR5/4); micaceous; fine-grained; case hardened; bioturbated; forms a bench.   0.8

21   Shale; grayish orange pink (5YR7/4); not calcareous.   0.1

20   Sandstone; pale greenish yellow (10Y8/2); very fine-grained quartzarenite; micaceous; not calcareous; trough crossbedded; forms a thick slope.   17.9

19   Sandstone; dusky yellow (5Y6/4) to dark yellowish orange (10YR6/6); very fine-grained; limonitic; not calcareous.   1.0

Chilikta Formation:

18   Shale; moderate olive brown (5Y4/4) and light olive brown (5Y5/6); papery; not calcareous; weathers green; contains ostracods.   0.8

17   Sandstone and shale in thin interbeds, sandstone dominant; shale is same color and lithology as unit 16; sandstone is grayish yellow (5Y8/4) and yellowish gray (5Y7/2); fine-grained quartzarenite; micaceous; not calcareous; laminated.   2.3

16   Shale; grayish orange pink (5YR7/2) to pale yellowish brown (10YR6/2); not calcareous; laminated; plant fossils rarer here than in lower units.   2.9

15   Sandstone; yellowish gray (5Y7/2) to grayish yellow (5Y8/4); fine-grained, well-sorted quartzarenite; clayey; micaceous; not calcareous; laminated; sulfurous.   0.4

14   Sandstone and shale; same colors and lithologies as unit 12.   4.2

13   Sandy shale; same colors and lithology as unit 11 but with more shale.   1.9

12   Sandstone and shale in thin laminae; pale yellowish brown (10YR6/2); sandstone is very fine-grained quartzarenite; micaceous; limonitic; thicker beds but ripple-laminated like unit 11; not calcareous.   0.7

11   Sandy shale; grayish orange pink (5YR7/2) to pale yellowish brown (10YR6/2); limonitic parts are dark yellowish orange (10YR6/6) and pale yellowish orange (10YR8/6); plant debris throughout; laminated; not calcareous.   2.7

10   Sandstone; dark yellowish brown (10YR4/2) to dusky yellowish brown (10YR2/2); fine-grained, limonitic; trough crossbedded; forms a ledge or bench like unit 5; contains sharks teeth (large lamniforms) and bone fragments (Glikman, 1964).   0.4

9   Sandstone; same colors and lithology as unit 6.   1.6

8   Clayey sandstone; dark yellowish orange (10YR6/6) to moderate yellowish brown (10YR5/4); very fine-grained; very limonitic; not calcareous.   1.1

7   Sandstone; same colors and lithology as unit 6 but without limonite nodules or crust; weathers very pale orange.   2.7

6   Sandstone; grayish orange (10YR7/4) to moderate yellowish brown (10YR5/4) with magnesium-rich parts that are dusky yellowish brown (10YR2/2); very fine-grained, clayey litharenite; limonitic; contains limonite nodules up to 1 m across; capped by a limonitic crust 0.1 m thick.   1.0

Kutanbulak Formation:

5   Limonitic sandstone; moderate yellowish brown (10YR5/4) and dark yellowish brown (10YR4/2); very dense; forms a ledge.   0.2

4   Sandstone; yellowish gray (5Y8/1) and light olive gray (5Y6/1); very fine-grained quartzarenite; slightly micaceous; low angle crossbeds.   4.3

3   Sandstone; yellowish gray (5Y7/2) to dusky yellow (5Y6/4); more micaceous than unit 2; thinly laminated; fine-grained subrounded quartzarenite; laminated to ripple laminated.   14.9

2   Sandstone; yellowish gray (5Y7/2) to very pale orange (10YR8/2) with dark yellowish orange (10YR6/6) and dusky yellowish brown

(10YR2/2) limonitic portions; fine-grained, subrounded quartzarenite; micaceous; very friable; trough crossbedded with some steep foresets; laminated to ripple laminated; some fist-sized Mn-rich concretions.   8.9

Chegan Formation:
1 Shale; grayish olive (10Y4/2); not calcareous; very thin laminae   not measured

B—Kumbulak PIN Quarry

Section measured at PIN excavation. Section begins at UTM 41316964E, 5185191N, and ends at PIN excavation, 41316737E, 5185226N. Strata are treated as flat-lying. This is the location of Orlov's (1939) series of excavations.

Unit	Lithology	Thickness (m)

Aral Formation:
18 Sandy limestone; same colors and lithology as unit 15; laminated; thick bedded; *Corbula*-bearing; top of PIN quarry.   2.8+

17 Mudstone; pale olive (10Y6/2); calcareous; similar to unit 16 but with calcrete nodules; skull *Paraceratherium*.   1.2

16 Mudstone; pale olive (10Y6/2); postcrania *Paraceratherium*.   0.8

15 Sandy limestone; pale greenish yellow (10Y8/2) to white (N9); *Corbula* coquina in lenses; well-indurated; very calcareous; thickly bedded.   1.2

14 Sandy claystone; light greenish gray (5GY8/1).   1.4

Chagray Formation:
13 Sandstone; same colors and lithology as unit 6; some cover.   4.2

12 Limonite crust; same color and lithology as unit 3.   0.1

11 Sandstone; same colors and lithology as unit 6.   0.9

10 Limonite crust; same colors and lithology as unit 3.   0.1

9 Sandy mudstone and muddy sandstone; light greenish gray (5GY8/1) to yellow gray (5Y8/1); not calcareous.   0.7

8 Sandstone; same colors and lithology as units 6 and 2; some cover.   11.5

7 Sandstone; yellowish gray (5Y7/2 and 5Y8/1);

fine-grained quartzarenite; micaceous; not calcareous; indurated; laminated to hummocky-bedded; forms a ledge.   0.2

6 Sandstone; yellowish gray (5Y8/1) with grayish orange (10YR7/4) to dark yellowish orange (10YR6/6) limonitic portions; fine- to medium-grained litharenite; very micaceous; not calcareous; much cover.   14.0

5 Limonite crust; same colors and lithology as unit 3; contains sharks' teeth and oxidized logs.   0.2

4 Sandstone; same colors and lithology as unit 2.   0.8

3 Limonitic sandstone crust; dark yellowish orange (10YR6/6), dusky yellowish brown (10YR2/2), and dark yellowish brown (10YR4/2); fine-grained.   0.1

2 Sandstone; very pale orange (10YR8/2) with dark yellowish orange (10YR6/6) mottles; very fine-grained, clayey quartzarenite; not calcareous; laminated; limonitic; friable.   2.7

Chilikta Formation:
1 Shale; pinkish gray (5YR8/1) to light brownish gray (5YR6/1).   not measured

C—Kumbulak Akespe

Section begins at UTM 41314843E, 5186208N, not far above the unexposed base of the Kutanbulak Formation, and ends at locality 4 at 41315113E, 5186634N.

Unit	Lithology	Thickness (m)

Aral Formation:
27 Sandstone; white (N9); calcareous; ripple-laminated and hummocky; *Corbula*.   0.5

26 Silty mudstone; pale olive (10Y6/2). "*Gigantamynodon*" *akespensis* site is 2.5 m above base of this unit.   4.0

25 Mudstone and calcareous mudstone; interbedded light greenish gray (5GY/1) (calcareous) and pale olive (10Y6/2).   0.9

Chagray Formation:
24 Sandstone; light greenish gray (5GY8/1) to yellowish gray (5Y8/1); same lithology as unit 23.   2.6

23 Sandstone; yellowish gray (5Y8/1) to grayish orange (10YR7/4); limonitic; trough crossbedded; forms a much covered slope; better ex-

posures reveal thin limonite lenses every few meters.   14.4

22 Sandstone; dark yellowish orange (10YR6/6); ripple laminated; bioturbated; forms a ledge.   0.3

21 Sandstone slope; much covered; same color and lithology as unit 13.   1.7

20 Limonite; same color and lithology as unit 14.   0.1

19 Sandstone; same color and lithology as unit 13.   0.9

18 Limonite; same color and lithology as unit 14.   0.2

17 Sandstone; same color and lithology as unit 13; much cover.   5.0

16 Limonite; same color and lithology as unit 14.   0.2

15 Sandstone; same color and lithology as unit 13.   1.5

14 Limonite; ripple laminated.   0.3

13 Sandstone; white (N9) to yellowish gray (5Y8/1); fine-grained quartzarenite; trough crossbedded.   1.8

12 Sandstone; dark yellowish orange (10YR6/6); very limonitic; trough crossbedded; forms a ledge; this unit and unit 13 above sometimes scour through underlying units as far as units 9 and 10.   0.3

Chilikta Formation:
11 Silty shale; same color and lithology as unit 9; plant-bearing beds with *Taxodium* located 2 m above base at UTM 4133147554E, 5186349N.   5.8

10 Sandstone; yellowish gray (5Y7/2); limonitic; crossbedded.   0.5

9   Silty shale; grayish orange pink (5R7/2); laminated.   2.4

8   Sandstone; same color and lithology as unit 6.   0.3

7   Sandstone; same color and lithology as unit 5.   0.8

6   Sandstone; dark yellowish orange (10YR6/6); ripple laminated; well-indurated; forms a bench.   0.7

5   Sandstone; moderate yellowish brown (10YR5/4) and dark yellowish orange (10YR6/6); similar lithology to unit 4 except much more limonitic.   2.3

4   Sandstone; pale greenish yellow (10Y8/2) to white (N9); with limonite plates at approximately 0.5 m intervals; friable.   3.0

3   Limonitic sandstone; moderate yellowish brown (10YR5/4) to dark yellowish orange (10YR6/6); forms a ledge; this is the basal marker bed of the Chilikta.   0.6

Kutanbulak Formation:
2   Sandstone; similar colors and lithologies to unit 1, but with pale greenish yellow (10Y8/2); large (0.9 m diameter) limonitic cannonball concretions.   5.0

1   Sandstone; complex multistoried unit; laminated to ripple laminated with local herringbones in steep (approximately 20° dip) cliniforms; foresets dip to the southeast; limonite on laminae; much cut and fill.   18.4

D—Altyn Chokysu V Plant Locality

Section begins at UTM 41350813E, 5237456N and ends at uppermost escarpment at 41350801E, 5237784N. Strata dip approximately 3° and are treated as flat-lying.

Unit	Lithology	Thickness (m)

Aral Formation:
47 Limestone; very pale orange (10YR8/2); *Corbula* molds in micrite matrix; locally coquinoid; forms a caprock.   0.5+

46 Clayey sandstone; white (N9) to very pale orange (10YR8/2); very fine- to fine-grained carbonate sand; very calcareous; ripple laminated; very friable; *Paraceratherium* postcrania. 1.3

45 Shale; same color and lithology as unit 37; Lopatin's (1994b) bone level IV ~2.0 m above base.   4.1

44 Mudstone; grayish yellow green (5GY7/2) with brown limonite mottles.   1.5

43 Clayey sandstone; yellowish gray (5Y8/1); friable; limonitic.   1.0

42 Shale; same color and lithology as unit 36.   0.4

41 Shale; same color and lithology as unit 37.   0.7

40 Shale; same color and lithology as unit 36 with limonite band in middle. 0.7

39 Shale; same color and lithology as unit 37. 0.6

38 Shale; same color and lithology as unit 36. 0.9

37 Shale; grayish yellow green (5GY7/2); calcareous. 0.8

36 Shale; pale greenish yellow (10Y8/2); very calcareous. 1.7

35 Mudstone; same color and lithology as unit 31. 0.3

34 Shale; same color and lithology as unit 24. 0.9

33 Limonite; same color and lithology as unit 7. <0.1

32 Shale; same color and lithology as unit 24. 1.1

31 Mudstone; grayish yellow (5Y8/4) to moderate yellow (5Y7/5); very indurated; slightly calcareous; laminated. 1.5

30 Shale; same color and lithology as unit 24. 1.3

29 Shale; same color and lithology as unit 25 but more discontinuous; occurs in lenses 2–5 m long. 0.2

28 Shale; same color and lithology as unit 24. 1.0

27 Shale; same color and lithology as unit 25. 0.2

26 Shale; same color and lithology as unit 24. 1.1

25 Shale; yellowish gray (5Y7/2) to pale olive (10Y6/2); *Corbula* are white (N9); very calcareous; this is the main *Corbula* coquina; units 25–28 above are Lopatin's (1994*b*) level II. 0.8

24 Shale; grayish yellow green (5GY7/2) with dark yellowish orange (10YR6/6) mottling; slightly calcareous; basal bone bed of Lopatin's (1994*b*) level I at base of this unit. 1.5

Chagray Formation:
23 Shale; yellowish gray (5Y8/1) to light greenish gray (5GY8/1); kaolinitic; not calcareous; laminated. 1.3

22 Sandstone; very pale orange (10YR8/2) and pale greenish yellow (10Y8/2); very fine-grained quartzarenite; clayey; not calcareous; massive. 1.5

21 Thin (0.2–0.4 m) interbeds of units 19 and 20 colors and lithologies. 2.5

20 Shale with sandstone laminae like unit 19; grayish yellow (5Y8/4); not calcareous; sandstones have unit 19 colors. 0.4

19 Sandstone; very pale orange (10YR8/2) with dark yellowish orange (10YR6/6) streaks; very fine- to fine-grained quartzarenite; limonitic; slightly micaceous; not calcareous; laminar to trough crossbedded; soft. 1.9

Chilikta Formation:
18 Sandy shale; dusky yellow (5Y6/4); not calcareous. 0.7

17 Sandstone; same colors and lithology as unit 15. 1.1

16 Limonite crust; same color and lithology as unit 7. >0.1

15 Sandstone; yellowish gray (5Y7/2) to grayish yellow (5Y8/4); very fine-grained, well-sorted quartzarenite; slightly micaceous; limonitic; not calcareous. 2.8

14 Silty shale; pale yellowish orange (10YR8/6) to dark yellowish orange (10YR6/6); not calcareous. 0.8

13 Shale; pale olive (10Y6/2); ostracods. 1.3

12 Sandy siltstone; yellowish gray (5Y7/2) and grayish yellow (5Y8/4); micaceous; not calcareous; laminar. 1.3

11 Sandy siltstone; pinkish gray (5YR8/1) and grayish orange pink (5YR7/2); not calcareous; trough crossbedded. 1.5

10 Sandstone; very pale orange (10YR8/2) with dark yellowish orange (10YR6/6) and pale yellowish orange (10YR8/6) mottles; fine-grained, well-sorted quartzarenite; much limonite; slightly micaceous; not calcareous; hematitic; friable; trough crossbedded. 1.9

9 Limonite; same color and lithology as unit 7. 0.05

8 Silty/sandy shale; pinkish gray (5YR8/1) and grayish orange pink (5YR7/2); thinly laminat-

ed; gypsum rosettes; lower 3 m has Altyn Chokysu V plant beds.   4.6

7   Limonite; moderate yellowish brown (10YR5/4) and dark yellowish orange (10YR6/6) with dusky yellowish brown (10YR2/2) Mn-rich blebs.   0.05

6   Siltstone; same color and lithology as unit 4.   1.0

5   Limonite; same color and lithology as unit 7.   0.05

4   Siltstone; pinkish gray (5YR8/1); laminated; not calcareous.   0.9

Kutanbulak Formation:

3   Prominent limonitic brown/black crust with plant stems; indurated.   0.1

2   Sandstone; very pale orange (10YR8/2) with limonite of grayish orange (10YR7/4) and dark yellowish orange (10YR6/6); fine-grained, well-sorted quartzarenite; much limonite; slightly micaceous; not calcareous; some ripples; friable.   1.9

Chegan Formation:

1   Silty shale; dusky yellow green (5GY7/2); siderite nodules are light brownish gray (5YR6/1) and pale yellowish brown (10YR6/2); calcareous; gastropods and bivalves.   7.5+

E—Chokysu Vertebrate Locality

Section begins at UTM 41357371E, 5238795N and ends at 41357557E, 5239091N (Bendukize's Chokysu site).

Unit	Lithology	Thickness (m)

Aral Formation:

52   Sandstone; ripple laminated and trough cross-bedded; forms an escarpment-capping ledge.   0.8+

51   Shale; same color and lithology as unit 49; this is Bendukidze's (1993) Chokysu site level.   2.2

50   Shale; pale olive (10Y6/2).   1.5

49   Shale; grayish yellow green (5GY7/2).   0.4

48   Shale; pale olive (10Y6/2).   0.9

47   Limestone; white (N9); forms a ledge.   0.3

46   Shale; grayish yellow green (5GY7/2).   1.4

45   Shale; pale olive (10Y6/2).   1.5

44   Shale, grayish yellow green (5GY7/2).   1.2

43   Limestone; white (N9); forms a prominent ledge.   0.6

42   Claystone; same color and lithology as unit 40.   1.2

41   Shale; same color and lithology as unit 39 with a carbonate ledge.   0.4

40   Claystone; pale olive (10Y6/2); very dark green band.   0.9

39   Shale; pale olive (10Y6/2).   2.0

38   Shale/claystone; grayish yellow green (5GY7/2); some lenses of *Corbula*; weathers to a popcorn texture.   4.2

Chagray Formation:

37   Silty sandstone; grayish yellow green (5GY7/2); very fine grained limonitic quartzarenite.   0.8

36   Siltstone; same color and lithology as unit 34.   0.9

35   Sandstone; grayish yellow green (5GY7/2); hummocky bedded.   0.3

34   Siltstone; pinkish gray (5YR8/1); laminated; lignitic; very Chilikta-like lithology.   0.3

33   Sandstone; yellowish gray (5Y7/2); limonitic; laminated.   1.3

32   Limonite; same color and lithology as unit 5.   0.1

31   Sandstone; same color and lithology as unit 29.   1.6

30   Limonite; same color and lithology as unit 5.   0.1

29   Sandstone; yellowish gray (5Y7/2); limonitic.   1.5

Chilikta Formation:

28   Shale; moderate yellowish brown (10YR4/2).   1.1

27   Shale; pale olive (10Y6/2); grades up via mottling into unit 28.   0.9

26   Shale; moderate yellowish brown (10YR4/2); Mn concretions.   0.8

25   Sandstone; same color and lithology as unit 23.   0.6

24   Shale; pale olive (10Y6/2).   0.6

23   Sandstone; white (N9); fine-grained; unit con-

tains *Paraceratherium* tooth fragments (Lucas and Emry, 1996*a*) and sirenian rib fragments. 1.2

22 Sandstone; moderate yellowish brown (10YR4/2); ferruginous; ripple laminated; well-indurated; forms a ledge; pinches out approximately 100 m to the north of section. 0.2–0.3

21 Sandstone; white (N9); fine- to medium-grained quartzarenite; laminated; = unit 11 sandstone at Sary-Oba (section H). 1.4

20 Sandy siltstone; same color and lithology as unit 16. 0.8

19 Limonite; same color and lithology as unit 5. <0.1

18 Silty shale; moderate yellowish brown (10YR4/2); lignitic. 0.9

17 Limonite; same color and lithology as unit 5. <0.1

16 Sandy siltstone; pinkish gray (5YR8/1); laminated. 1.0

15 Limonite; same color and lithology as unit 5. <0.1

14 Siltstone; same color and lithology as unit 4. 0.3

13 Limonite; same color and lithology as unit 5. <0.1

12 Siltstone; same color and lithology as unit 4. 0.5

11 Limonite; same color and lithology as unit 5. <0.1

10 Siltstone; same color and lithology as unit 4. 0.5

9 Limonite; same color and lithology as unit 5. 0.1

8 Siltstone; same color and lithology as unit 4. 1.5

7 Limonite; same color and lithology as unit 5. 0.1

6 Siltstone; same color and lithology as unit 4. 1.3

5 Limonite; moderate yellowish brown (10YR5/4) and dark yellowish orange

(10YR6/6) with dusky yellowish brown (10YR2/2) Mn-rich blebs. 0.1

4 Siltstone; moderate yellowish brown (10YR5/4); laminated. 1.5

Kutanbulak Formation:
3 Sandstone; dark yellowish orange (10YR6/6) and dusky yellowish brown (10YR2/2); limonitic; forms a prominent ledge. 1.4

2 Sandstone; grayish yellow (5Y8/4); limonitic; friable; slope former. 5.8

Chegan Formation:
1 Shale; grayish olive (10Y4/2). not measured

F— *Nelumbo* Site

Section begins at UTM 41352212E, 5237576N, and ends at 41352064E, 5237797N. This is the Altyn Chokysu II plant locality of Andreyev (1991).

Unit   Lithology   Thickness (m)
Aral Formation:
29 Shale; light greenish gray (5GY8/12); top of hill. 0.8+

28 Shale; pale olive (10Y6/2). 2.4

27 Shale; variegated moderate yellowish brown (10YR5/4) and light greenish gray (5GY8/1). 2.3

26 Shale; light greenish gray (5GY8/1). 1.6

25 Shale; pale olive (10Y6/2). 0.6

24 Shale; light greenish gray (5GY8/1). 2.7

23 Mudstone; grayish yellow (5Y8/4); well indurated; forms a ledge. 0.2

22 Shale; light greenish gray (5GY8/1). 1.1

21 Shale; pale olive (10Y6/2). 1.1

20 Shale; light greenish gray (5GY8/1). 1.5

19 Claystone; light greenish gray (5GY8/1) with lenses of *Corbula*. 1.2

18 *Corbula* bed; white (N9); laterally continuous (locally). 0.1

17 Shale; light greenish gray (5GY8/1). 0.9

16 Claystone; pale olive (10Y6/2); base of first *Corbula* bed. 0.8

15 Shale; light greenish gray (5GY8/1); bone lag at base. 0.9

Chagray Formation:

14   Sandstone; same colors and lithology as unit 13 but more shaley.   1.1

13   Sandstone; same colors and lithology as unit 11.   1.5

12   Shaley sandstone; light greenish gray (5GY8/1) to moderate yellowish brown (10YR5/4); laminated.   1.3

11   Sandstone; very pale orange (10YR8/2), weathers pale yellowish brown (10YR6/2); very fine- to fine-grained quartzarenite; micaceous; limonitic; not calcareous; laminated.   3.6

Chilikta Formation:

10   Silty shale; pale yellowish brown (10YR6/2) fresh, weathers pinkish gray (5YR8/1); not calcareous; limonitic layers; *Nelumbo* lens (Altyn Chokysu locality II).   1.9

9   Shale; pale olive (10Y6/2); ostracods, bone fragments.   1.4

8   Sandstone; yellowish gray (5Y8/1) to light greenish gray (5GY8/1), limonitic parts are dark yellowish orange (10YR6/6) and moderate yellowish brown (10YR5/4); fine-grained quartzarenite; slightly micaceous.   1.3

7   Siltstone; light greenish gray (5GY8/1); blocky.   0.6

6   Limonite crust; moderate yellowish brown (10YR5/4) and dark yellowish orange (10YR6/6); well-indurated.   0.4

5   Sandy siltstone; yellowish gray (5Y8/1); not calcareous; soft; laminated.   1.5

4   Sandstone and siltstone; same colors and lithologies as unit 2.   0.7

3   Shale with minor sandstone; pinkish gray (5YR8/1) to grayish orange pink (5YR7/2) with dark yellowish orange (10YR6/6) and dusky yellowish brown (10YR2/2) limonite; not calcareous; plant producing level.   3.7

2   Sandstone and siltstone; pinkish gray (5YR8/1) to grayish orange pink (5YR7/2); sandstone is fine-grained quartzarenite; limonitic on some layers; interbedded with siltstone in 2–3 mm thick sets; not calcareous; laminated.   4.4

Chegan Formation:

1   Shale; pale olive (10Y6/2).   not measured

G—Aktau Mountain

Section measured at UTM 41336840E, 5247342N on the southwestern slope of Aktau Mountain. Strata are flat-lying.

Unit	Lithology	Thickness (m)

Aral Formation:

14   Sandstone; ripple laminated; caps ridge; = top Aral sandstone of section E (unit 52).   0.2+

13   Shale; pale olive (10Y6/2); slope; some cover; Bendukidze's (1993) "Akotau" site 1.3 m below top of unit.   5.4

12   Shale; pale olive (10Y6/2) with limonite concretions.   0.4

11   Shale; light greenish gray (5GY8/1) with thin bands of pale olive (10Y6/2).   3.7

10   Mudstone; grayish yellow (5GY7/2); calcareous; forms a ledge.   0.6

9   Shale; pale olive (10Y6/2).   1.2

8   Shale; light greenish gray (5GY8/1).   1.3

7   Shale; pale olive (10Y6/2).   1.2

6   *Corbula* lens; white (N9).   0.2

5   Shale; pale olive (10Y6/2).   0.9

4   Thick *Corbula* lens with bone fragments; white (N9).   0.4

3   Shale; pale olive (10Y6/2); base is bone bed with *Corbula*.   1.9

Chagray Formation:

2   Sandstone; white (N9), clayey, laminated.   1.3

1   Sandstone; moderate yellowish brown (10YR4/2); limonitic crust.   not measured

H—Sary-Oba

Sary-Oba plant locale (Altyn Chokysu VI). Section measured on point to west of triangulation station at UTM 41360401E, 5240567N with section traversing from south to north. Strata dip 2° to ~N and are treated as flat-lying.

Unit	Lithology	Thickness (m)

Chilikta Formation:

13   Limey sandstone (calcarenite); yellowish gray (5Y8/1); indurated.   0.8+

12   Shale; moderate brown (5YR4/4) to light olive brown (5Y5/6); calcareous; forms a slope.   2.0

11   Sandstone; same colors and lithology as unit 9.   2.0

10   Sandy mudstone; mostly pale olive (10Y6/2) with some olive gray (5Y4/1); slightly calcareous; upper half is Mg-rich to carbonaceous.   0.5

9   Sandstone; dark yellowish orange (10YR6/6); fine- to medium-grained, poorly sorted limonite; slightly micaceous; not calcareous; friable.   1.2

8   Sandstone; same color and lithology as unit 6.   <0.1

7   Sandstone; same color and lithology as unit 5.   0.4

6   Sandstone; grayish orange (10YR7/4) to dark yellowish orange (10YR6/6); dense; limonitic; not calcareous; essentially a limonite crust.   0.1

5   Sandstone; grayish yellow (5Y8/4); very fine-grained quartzarenite; slightly micaceous; not calcareous; poorly indurated; forms a slope.   2.7

4   Sandstone;   moderate   yellowish   brown (10YR5/4) to dark yellowish brown (10YR4/2); fine-grained, subangular, well-sorted quartzarenite; very limonitic; slightly micaceous; not calcareous; ripple laminated; forms an indurated ledge that serves as a marker bed; Sary-Oba plant locality (Altyn Chokysu VI) at ~top of unit.   0.8

Kutanbulak Formation:
3   Sandy siltstone; dark yellowish orange (10YR6/6) to moderate yellowish brown (10YR5/4); limonitic; not calcareous; soft; some ripple laminae; this is a weathering feature of top bed of Kutanbulak; locally becomes just like unit 4.   1.4

2   Sandstone; grayish yellow (5Y8/4) with dark yellowish orange (10YR4/2) limonitic streaks; very fine- to medium-grained, subangular limonite; not calcareous; laminated; about 2 m from top of unit a 1-m-thick band of limonitic sandstone forms an orange band; cliff.   16.3

Chegan Formation:
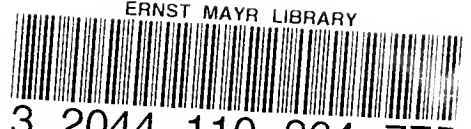1   Silty shale; dusky yellow green (5GY7/2).   not measured